University of Alberta

Systematics of the most ancient conifers

by

Genaro Rodrigo Hernandez Castillo

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the

requirements for the degree of *Doctor of Philosophy*

in

Systematics and Evolution

Department of *Biological Sciences*

Edmonton, Alberta

Spring 2006

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Your file Votre référence
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ISBN: 0-494-13987-0

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To my family, friends, and colleagues

ABSTRACT

This dissertation explores a new methodology to account for ranges of variation within species of fossil conifers using mutivariate analyses. This methodology provides a framework for understanding growth architecture of fossil conifers and is calibrated using a comparison to juvenile trees of extant *Araucaria heterophylla* (Salisb.) Franco. Three new, whole plant reconstructions from the Upper Pennsylvanian of Kansas are presented, and the family Emporiaceae, the genus *Emporia* and the type species for the family, *Emporia lockardii*, emended. The new species are based on lateral branches, pollen cones and ovulate cones that are correlated by organic connection and by morphological, cuticular, and anatomical evidence. They provide the earliest evidence of age-dependent heterophylly in ancient conifers and support previous ideas on the reproductive biology of Paleozoic conifers. The Emporiaceae is the only family of primitive conifers known as complete plants, as well as one of the two families where all cuticles of leaves and leaf-like structures have been fully analyzed. This study confirms that cuticles from isolated and/or fragmentary branches, where no organic connections occur and small numbers of specimens are known, cannot be used to accurately identify walchian conifer plants. Phylogenetic analysis of the most primitive conifers suggests a single clade that includes all of the most ancient conifers and places them as sister to Cordaitales and a transitional conifer-like *Vojnovskya* plant. However, the base of the Voltziales clade is characterized by a polytomy that includes Angaran and Gondwanan conifers, and *Thucydia* with *Ernestiodendron* at the base of a paraphyletic assemblage of Euramerican conifers.

Results of this dissertation further refine our interpretations of Paleozoic conifers and

proposed sets of diagnostic characters for the reconstruction of the most primitive conifers. An appreciation for these characters derived from complete reconstructions would greatly enhance our knowledge of fossil conifers. Current familial circumscriptions need to be modified so that clear diagnostic characters can be defined at the family level among fossil conifers. Even though our present knowledge of the most primitive conifers has improved greatly, we still lack synapomorphies that unite extinct and extant conifers.

ACKNOWLEDGMENTS

I would like to thank my committee, Dr. Randy Currah, Dr. Michael Caldwell, Dr. Alexander P. Wolfe, Professor Dr. Hans Kerp, and especially my supervisor Dr. Ruth A. Stockey for her support, invaluable help at all times, and the sushi. I want to express my gratitude to Drs. Gar W. Rothwell, Gene Mapes, and Royal Mapes (Ohio University) for their invaluable help, support and enthusiasm collecting hundreds of excellently preserved fossil conifers from the Hamilton Quarry. As I said before, they deserved all the credit for the Hamilton Quarry collection, I am just here catching a ride, thank you, guys. I would also like to thank Dr. Sean W. Graham (University of British Columbia), the Paleobotany gang: Stefan A Little, Selena Y. Smith, Brian Rankin, Simone Mageau, Kirstin Brink; and I would like to extended my gratitude to Randal Mindell for his help, support, valuable comments, and inspiring editing. I would also like to thank Jeffrey M. Saarela (University of British Columbia), Dr. Michael Dunn (Cameron University), Dr. Mihai Florian Alexandru Tomescu (Humboldt University), Alejandra de Villa Meza (UNAM) and Veronica Zamora Gutierrez (Universidad de Guadalajara) for their support at different stages of this dissertation.

This project was made possible by a number of people and institutions throughout the world that provided guidance, support, access to collections and equipment, references, live specimens, and help in finding my way around in different countries in search for fossil and living conifers. They are included the following paragraphs.

In Australia: John G. Douglas and Tom O'Sullivan (Warrnambool, Victoria); Lance Carr (Mountain Range Nursery, Woonona, New South Wales); Ian A. Smith (Queensland Museum, Queensland). In the Czech Republic: Jiří Kvaček, Milan Libertín, and Renata Patova (Národní Muzeum, Prague), Zbyněk Šimůnek (Český Geologický Ústav, Prague). In France: Jean Broutin and Thanh Thuy Nguyen Tu (Université Pierre et Marie Curie, Paris); Jean Dejax and Dario De Franceschi (Muséum National d'Histoire Naturelle, Paris); Jean Galtier, Brigitte Meyer-Berthaud, and Nick Rowe (CNRS, Montpellier); Léa Grauvogel-Stamm (Université L. Pasteur, Strasbourg); Georges Barale and Véronique Daviero (Université Claude Bernard Lyon 1, Villeurbanne);

In Germany: Hans Kerp, Martine Berthelin, Sunia Lausberg, Hagen Hass (Westfälische Wilhelms University, Münster); Stephan Schultka (Naturhistorisches Forschungsinstitut, Museum für Naturkunde, Zentralinstitut der Humboldt-Universität, Berlin); Ralf Wernerburg (Naturhistorisches Museum, Schloß Bertholdsburg, Schleusingen); Thomas Martens (Museum der Natur, Gotha); Lutz and Carola Kunzmann (Staatliches Museum für Mineralogie und Geologie, Dresden); Harald Stapf and Arnulf Stapf (Paläontologisches Museum, Nierstein); Dieter Uhl (Institut für Geowissenschaften, Tübingen); Michael Krings (Bayerische Staatssammlung für Paläontologie und Geologie, München); Volker Wilde (Forschungsinstitut Senckenberg, Frankfurt am Main); Ronny Rößler and Ramona Schwab (Museum für Naturkunde Chemnitz); Robert Noll (Tiefenthal). In the Netherlands: Johanna H. A. van Konijnenburg-van Cittert and J. van der Burgh (Departement Palaeobotanie en Palynologie, Universiteit Utrecht). In Sweden: Else Marie Friis, Thomas Denk and Kamlesh Khullar (Naturhistoriska Riksmuseet, Stockholm). In the United Kingdom: Andrew C. Scott, Margaret Collinson, and Nicholas P. Sille (Geology Department, Royal Holloway University of London, Egham, Surrey), Jason Hilton (University of Birmingham), Paul Kenrick (Department of Palaeontology, The Natural History

Museum, London).

This work was supported in part by the Consejo Nacional de Ciencia y Tecnología (CONACYT) in Mexico (Grant 128361), Department of Biological Sciences and Faculty of Graduate Studies and Research (University of Alberta), and by the Natural Sciences and Engineering Research Council of Canada (Grant A-6908 to Ruth A. Stockey), and the National Science Foundation (Grant DEB-9527920 to Gar W. Rothwell and Gene Mapes).

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CHAPTER 1

General introduction

Introduction

Conifers have played a major role in terrestrial ecosystems throughout the world since the end of Paleozoic, however, knowledge of the most primitive conifers is scarce and confusing. Primitive conifers colloquially known as "walchian" conifers have been described from Upper Carboniferous (Pennsylvanian) and Permian deposits of Europe, North America, and North Africa (Florin 1938-45; Clement-Westerhof 1984, 1987; Kerp et al. 1990; Mapes and Rothwell 1991). Most early descriptions are of European specimens (Dijkstra 1975), where specimens are based primarily on morphological characters of isolated vegetative branches (Göeppert 1850, 1864-1865; Geinitz 1880; Florin 1938-45; Visscher et al. 1986).

The first specimens of ancient conifers were either described as species of *Walchia* Sternberg (1825), or were misidentified as belonging to another taxonomic group (Florin 1938-45; Kerp et al. 1990; Kerp and Clement-Westerhof 1991). Most descriptions were based solely on morphological characters of isolated remains usually belonging to fragmentary vegetative branches. It was Rudolf Florin (1927, 1938-45, 1950, 1951) who created a new taxonomic approach based on morphological and cuticular characters of the most ancient conifers. He attempted to base species on both vegetative and fertile organs (Florin 1927, 1938-45). However, all species were described primarily from vegetative shoots, with ovulate and pollen cones assigned to species later. Furthermore, no specific sets of characters were identified to support organ associations, and ranges of variation among species overlapped considerably. Morphological variation among these species was not assessed at that time. Moreover, all of these species came from mixed assemblages of conifers, where more than one species of conifer occurred at a locality, and accurate identification of species by small fragments of the plant is questionable.

In addition, new taxonomic concepts were created following the “promotion” of species approach (Visscher et al. 1986) in order to distinguish between “artificial” and “natural” genera. However, this new approach violated the rules of botanical nomenclature (ICBN) and lead to nomenclatural instability (Mapes and Rothwell 1991).

At present, there are no sets of diagnostic characters for most described species, and ranges of variation among specimens assigned to these species overlap considerably. Most species are based on vegetative organs, but genera and families are based on fertile structures (Florin 1938-45; Kerp and Clement-Westerhof 1991; Hernandez-Castillo et al. 2001). Moreover, the associations of vegetative and fertile organs are weak due to the lack of organic connection, absence of diagnostic characters, and their occurrence in mixed conifer assemblages. This situation is further complicated by nomenclatural irregularities that have led to a great deal of confusion and disagreement regarding the legitimate names for some of the most well known genera and species. Therefore, all previous taxonomic approaches are inadequate. Consequently, most newly discovered specimens of primitive conifers cannot be assigned to a species with confidence.

The goals of this dissertation are to 1) test previous hypotheses of ancient conifer species by assessing ranges of variation among previously described specimens by Florin and determine if the species are distinct entities using previously developed characters; 2) determine ranges of variation and patterns of variation within a single species of conifer by means of multivariate analyses using extant *Araucaria heterophylla* and the fossil conifer *Thucydia mahoningensis* as growth architectural models; 3) develop new whole plant species for previously described and newly discovered species walchian conifers from Europe, North Africa and North America; and 4) employ numerical cladistic analyses of morphological characters to infer systematic relationships among the most ancient conifers.

The use of multivariate techniques has been developed and tested in the description and analysis of one benchmark primitive conifer species, *Thucydia mahoningensis*, from the Upper Pennsylvanian of North America (Hernandez-Castillo et al. 2001). This conifer displays ranges of variation within a single species. Therefore, it was used to assess ranges of variation among extinct and extant conifers, using *Araucauria heterophylla* as an analogue for calibration. Initially, this approach was going to be employed to assess relationships of European fossil conifers that have long been regarded as the backbone of the primitive conifer classification. However, observation and reevaluation of most available European specimens gave preliminary results that indicated this course of study needed to be modified.

An extensive search was done to account for the most well-known walchian conifers in Europe and North America. Priority in this dissertation has been given to holotypes, paratypes and specimens figured by Florin (1938-45). Many of Florin's holotypes were located and many photographed by Dr. Gar W. Rothwell and Dr. Gene Mapes (Ohio University), and my supervisor Dr. Ruth A. Stockey. The remaining species and specimens were located and photographed at other museums and private collections throughout Europe by myself during the summers of 2002 and 2003. Important collections include the Muséum National d'Histoire Naturelle, Paris, the Université Montpellier II, Montpellier, the Naturhistorisches Forschungsinstitut, Museum für Naturkunde, Zentralinstitut der Humboldt-Universität, Berlin, the Naturhistorisches Museum, Schloß Bertholdsburg, Schleusingen, the Paläeontologishes Museum, Nierstein, Germany, and the Naturhistoriska Riksmuseet, Stockholm, Sweden. Despite the large number of specimens, their quality of preservation imposed restrictions on the taxa that could be used for multivariate analysis.

Chapters

Chapter 2 is divided into two sections. The first part of this chapter includes a statistical multivariate analysis of the lateral branches of *Thucydia mahoningensis* from the Upper Pennsylvanian of Ohio. This taxon was used because it is the only unequivocal walchian conifer known from the 7-11 mine locality in Ohio and, thus, ensures the presence of a single tree species. The second part of this chapter includes a statistical analysis of the ranges of variation in lateral branches of *Thucydia mahoningensis*, species of walchian conifers described by Florin (1938-45), and lateral branches of the living species *Araucaria heterophylla* (Salisb.) Franco (Norfolk Island Pine). *Araucaria heterophylla* was chosen for this analysis solely on its similar tree architecture that of walchian conifers (Florin 1950).

Chapters 3-5 include whole plant reconstructions of *Emporia lockardii* (Mapes et Rothwell) Mapes and Rothwell and two new species of walchian conifers from the Hamilton Quarry of Kansas. The Hamilton Quarry is east of Hamilton, Kansas, USA, secs. 5 and 8, T. 24 S., R. 12E., Virgil seven and a half foot quadrangle, Greenwood County, Kansas, U.S.A. (Fig. 1, chapters 3-5). Fossils occur in Late Pennsylvanian laminated carbonate mudstones of the Hartford Limestone Member, Topeka Limestone

Formation, Shawnee Group (Mapes and Rothwell, 1984; Bridge, 1988; French et al., 1988; Busch et al., 1988). The Topeka Limestone is the uppermost of the seven formations that make up the Shawnee Group. The Hartford Limestone is the most basal member this formation and overlies the Calhoun Shale (Maples 1988). The lenticular sandstones and argillaceous siltstones of the Calhoun Shale have been interpreted as indicators of a fluviodeltaic environment (French et al. 1988).

The Topeka Limestone represents the reestablishment of the marine conditions following the Calhoun deposition (French et al. 1988). The Hamilton Quarry locality in reality has three main quarry sites: Marlin, Willow Creek, and Main, that are located in the main channels of a north-to-south-trending paleochannel.in an estuarian environment under tidal influence (French et al. 1988; Fahrer et al., 1990; Fahrer, 1991; Feldman et al., 1993). This area is inferred to have been part of a southward-prograding barrier and tidal inlet system that fronted a fresh-to-brackish-water estuarine or lagoonal complex (French et al. 1988).

The specimens used in this study are coalified compressions with preserved cuticles and cellular permineralizations. The Hamilton Quarry has yielded approximately 4000 walchian conifer specimens that include nearly complete lateral branches, pollen cones and ovulate cones in addition to hundreds of isolated organs. Other gymnosperms found at this locality include Cordaitales, Medullosales and Callistophytales (Rothwell and Mapes 1988). However, walchian conifers represent about 50% of the fossils at this site. Floristic elements of typical Carboniferous coal swamp communities such as psaroniaceous tree ferns and lycopsids are rare or absent at this locality, and calamite remains are common only in a small area (Leisman et al. 1988;

Rothwell and Mapes 1988). Using sedimentological and taphonomic data combined with regional and local geology Rothwell and Mapes (1988) suggest that cordaitaleans may have formed part of the canopy of many dominant conifer communities with seed ferns forming part of the understory vegetation. Pteridophytic components of the flora may have been restricted to lowland lakes and stream-margins of the site. Moreover, previous analyses of the plants suggest that this community inhabited well-drained slopes at times of dropping sea levels and/or wide-spread aridity (Mapes and Rothwell 1988; Rothwell and Mapes 1988). Periods of aridity or water stress conditions are predicted by the presence of thick cuticles, sunken stomata, and needle-like leaves in conifers (Mapes and Rothwell 1988; Rothwell and Mapes 1988). Some of these characters have been used to infer xeric conditions in other fossil localities (e.g., Kerp et al. 1990).

Each plant reconstruction from the Hamilton Quarry presented here is based on dozens of specimens correlated by means of morphological, cuticular and anatomical features of lateral branches, pollen cones and ovulate cones. Each chapter includes an introduction, materials and methods, diagnosis, description, and discussion of the systematic relationships of the new taxa. Individual discussions include comparisons to other reconstructed conifers from Euramerica, and in the case of Chapter 3, an extended comparison with other ancient conifers worldwide was also included. Each chapter includes tables comparing vegetative and reproductive characters of previously described walchian conifers. Emphasis was placed on leaves of penultimate and ultimate shoots as well as ovulate cones or fertile zones. Additional tables that include morphological and cuticular characters of all leaves and leaf-like structures (i.e., cone bracts, microsporophylls) on the entire plant were also included. Thus, these reconstructions account for all organs of the plant and document ranges of variation among the characters most commonly used to typify walchian conifer species.

Chapter 6 includes numerical cladistic analyses of the most well-known walchian conifers worldwide. Conifers included are those where nearly complete plants or whole plant reconstructions are known. These reconstructions include taxa from Gondwana, Angara and Euramerica, and the species of Emporiaceae described in this thesis. These conifers range from Upper Pennsylvanian to Middle Triassic in age. Twenty-four taxa and 57 characters were used for these analyses.

The above results are summarized in Chapter 7. Conclusions are drawn on the validity of multivariate analyses in reconstructing fossil conifers, the utility of whole plant reconstructions, and the significance of individual sets of diagnostic characters. Suggestions for directions of future research on fossil conifers are given in light of the results of this dissertation.

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CHAPTER 2

Morphological variation of Euramerican walchian conifers

Introduction

The intention of this chapter was to assess ranges of variation in Euramerican Paleozoic conifers. At the inception of this work, our main goal was to use multivariate analyses to identify and distinguish species of walchian conifers to test the validity of species. Traditionally, conifers have been described based on a few morphological and cuticular characters. Most of the species known are described from fragmentary and isolated lateral branches (Florin, 1938-45), but correlating these specimens has always presented a challenge to paleobotanists. To date, these correlation techniques didn't work and only a few conifers are known as complete plants (e.g., *Otovicia hypnoides* Kerp, Poort, Swinkels et Verwer), while the large majority of the species are based on few specimens, many of which are often disarticulated and as such do not reflect all characters of the lateral branches.

Due to an overlap in morphological and cuticular characters in previously described species, a new approach was needed. Any approach used would need to account for a large number of characters that can be compared across several species. Statistical multivariate analyses are ideal in that they are designed to deal with several characters and numerous taxa at the same time (Kachigan 1986). Numerical analyses have been used previously to differentiate between species of fossil conifers (Alvin and Dalby 1987; Bertholon 1996), however these studies are limited by the number of taxa or characters.

The fourteen characters used in this analysis had been used in previous studies (e.g. Florin 1938-1945; Winston 1984; Bertholon 1996). Most of these characters were previously assessed in the description of *Thucydia mahonginensis* (Hernandez-Castillo

2000) and thus provide a framework for analyzing lateral branches of walchian conifers. While no multivariate analysis was undertaken for *Thucydia*, the characters used in its description proved useful for accounting for ranges of variation of the plant.

Most descriptions of these walchian conifers were based on specimens that were figured in Florin's monograph (1938-45). All holotypes and figured specimens from Florin's monograph were digitized. This triggered a search for more specimens throughout Europe to determine how many could be used for a numerical analysis of this kind. Two trips to Europe were made to different museums and universities that house walchian conifer specimens (Table 1). Over 3000 digital pictures of more than 700 specimens were taken. Preliminary measurements of figured specimens and holotypes were analyzed using multivariate analyses, but results lacked the resolution to distinguish species from one another. Thus, only the best preserved and most complete lateral branches of *Lebachia piniformis* Florin and *Ernestiodendron filiciforme* Florin were used in the analysis presented in this chapter. Due to the large amount of data, only a few examples of the spreadsheets used for this analysis are included at the end of this dissertation (Appendices 1-7).

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Chapter 2.1

The role of multivariate analyses in reconstructing fossil conifers

Introduction

The fossil record of conifers goes back to the Middle Pennsylvanian (Scott and Chaloner 1983; Galtier et al. 1992). Floras from the Upper Pennsylvanian and Permian have been characterized by a large number of conifer taxa. Our understanding of primitive conifers is based largely on the comprehensive studies of Florin (1927, 1938-45). More recently, many more conifer species from Euramerica and Cathaysia have been described (Clement-Westerhof 1987; Kerp et al. 1990; Mapes and Rothwell 1991; Yao et al. 2000), and some are now known as whole plants (Hernandez-Castillo et al. 2001).

Primitive conifers are usually preserved as coalified compressions that display morphological and cuticular features (Florin 1938-1945, 1950; Meyen, 1997; Clement-Westerhof 1984). Most fossil localities with primitive conifers have fragmentary and isolated conifer remains (Florin 1938-1945; Clement-Westerhof 1984, 1987; Kerp et al. 1990). However, some deposits generate exceptional conifer assemblages, with large numbers of exquisitely preserved specimens (Rothwell 1982; McComas 1988; Rothwell et al. 1997; Hernandez-Castillo 2000a). Many currently recognized genera and species of primitive conifers are based on a combination of shared morphological and cuticular characters present in isolated organs (Clement-Westerhof 1984, 1987; Kerp et al. 1990). However, morphological ranges of variation of isolated organs (e.g., leaves) are either overlapping or unknown for nearly all species (Hernandez-Castillo 2000a; Hernandez-Castillo et al. 2001), and not all cuticles on vegetative and reproductive organs in an individual conifer plant are the same (Hernandez-Castillo et al. 2001). Therefore, this current methodology for identifying species of primitive conifers is often unreliable.

The most reliable way to test hypotheses of species in primitive conifers is by the reconstruction of individual plants. Such reconstructions allow us to characterize fossil species and to produce a classification based on similar concepts to those of living plants. Therefore, primitive conifer plant reconstructions, where ranges of morphological and cuticular variation have been assessed, are needed.

Morphological and cuticular ranges of variation in shoots of primitive conifers are best known for *Thucydia mahoningensis* Hernandez-Castillo, Rothwell & Mapes (Hernandez-Castillo et al. 2001). Lateral branching systems, and leaves of *Thucydia* are similar to lateral branches of juvenile trees of *Araucaria heterophylla* (Salisb.) Franco. Both species have orthotropic stems with lateral plagiotropic branching systems that are covered by helically arranged simple leaves (Hernandez-Castillo et al. 2003). Therefore, *T. mahoningensis* is the ideal primitive conifer for analyzing ranges of variation, and for comparing the results to a living conifer with similar morphology (i.e., *A. heterophylla*) for the purpose of identifying isolated specimens of fossil conifers.

Materials and Methods

Thirteen specimens of *Thucydia mahoningensis* were used to assess ranges of variation of lateral plagiotropic branching systems (fig. 1) found at the abandoned 7-11 Mine locality in Columbiana County, Ohio, USA (McComas 1988; Hernandez-Castillo et al. 2001). This monotypic assemblage of conifer remains is preserved as coalified compressions/impressions and some specimens are also partly permineralized by pyrite. The age is most likely Desmoinesian (Westphalian D) or Missourian (late Stephanian A; McComas 1988), but may be as recent as Stephanian C or even Autunian (Wagner and Lyons 1997).

Three hundred and forty vegetative shoots including antepenultimate, penultimate and ultimate shoots are available for study (Hernandez-Castillo 2001). Thirteen specimens were chosen from the 39 most complete specimens that show penultimate and ultimate shoots in organic connection. Specimens were digitized using a Leaf Microlumina System, ver 1.2 (Westborough, MA). Digital images were stored as PSD files, and specimens were measured from the digital photographs of the lateral plagiotropic branches.

Five ultimate shoots were scored per specimen. Fourteen characters were recorded for each branching system (table 1), and ultimate shoots were measured from one side of each penultimate shoot (Hernandez-Castillo 2000b). When shoots were complete, measurements of the distal region were recorded one centimeter below the apex of the shoot to avoid inclusion of immature leaves. When branches were incomplete, morphological data were gathered from the most distal preserved region of the shoot.

Cluster and principal components analyses were performed. Basic data matrices of fossil specimens were created in NTSYS, ver. 2.1 for Windows (Rohlf 1993). Specimens were treated as columns, vegetative characters as rows. Numerical values of characters of the basic data matrices were standardized by subtracting the mean value of the character from each specimen from the average for this character over all specimens studied, and then dividing the resulting number by the standard deviation for this character in the sample. The same standardized matrix was used in both multivariate analyses. Cluster analysis was performed by calculating a similarity matrix between specimens using the Euclidean Distance Coefficient, and UPGMA (Sneath and Sokal

1973). Principal components analysis was performed with covariance matrices between characters calculated with Pearson's correlation index (Sneath and Sokal 1973).

Results

Thucydia mahoningensis has three orders of branching (antepenultimate, penultimate and ultimate) that bear helically arranged simple leaves (figs. 1A-C). The antepenultimate stem is orthtropic and wider than penultimate and ultimate shoots (figs. 1A). Lateral, plagiotropic, penultimate branches are symmetrical and they display three general shapes that have been described previously (Hernandez-Castillo et al. 2001). Two of the shapes are ovate (fig. 1B, 1G) and deltoid (fig 1C, 1H), and are analyzed in this multivariate study.

Cluster analyses of lateral plagiotropic branching systems of *T. mahoningensis* show two main clusters of specimens and an individual specimen (G8) separated from the rest of the fossils (fig. 2A). The first cluster ("a") is found at the top on the phenogram, and includes two subclusters (G1-G190 and G10-G25-G27) and an individual specimen (G158) (fig. 2A). The second cluster ("b") is composed of two main subclusters (G4, Gm2-G205, and G15-G16, G48) (fig. 2A).

Principal components analysis produces similar results to that of cluster analysis (figs. 2A- B). Two groups of lateral plagiotropic branches and specimen G8 are also recognized (fig. 2B). The first three components account for 67.98 % of the variation (table 2). The first component explains 34.02 % of the variation, while the second explains 19.50 % and the third only 14.45 % (table 2). A three dimensional graph shows how individual specimens are distributed (fig 2B). In this figure, both clusters share similar patterns to those of the cluster analysis; however characteristics of individual specimens are enhanced, and specimens display slightly different positions on the three axes (fig. 2B). Only two specimens (G25 and G8) are separated from the rest of the clusters. Specimen G25 is close to cluster "a" while G8 separated from the rest of the clusters (fig. 2B).

Two dimensional principal components graphs showing pairs of axes display clusters "a" and "b" (figs. 3A-C). In the first graph (PCA 1 vs PCA 2), most specimens are found at the top of the graph (fig. 3A). Specimen G8 is located at the right bottom of the graph (fig. 3A). The second graph (PCA 1 vs PCA 2) displays an evenly distributed arrangement of specimens across the entire graph (fig 3B). A third graph (PCA 1 vs PCA 3) shows a similar distribution to that observed in fig. 3A (fig. 3C). In this graph specimen G8 is again isolated from the rest of the specimens, and most specimens are located on the positive quadrant of PCA 2 (fig. 2).

The most highly positively correlated characters associated with the first component are angle 2 of leaves at the distal region of ultimate shoots, diameter of penultimate shoots at the basal region, and length of leaves at the proximal region of ultimate shoots (table 3, figs. 3A-B). While the second component is correlated to the diameter of ultimate shoots and the diameter of penultimate shoots at the apical region (table 3). Finally, the third component is correlated to the angle 2 of leaves at the proximal region of ultimate shoots and the length of penultimate shoots (table 3). Both PCA and CA show a similar cluster arrangements, but PCA character correlations complement results from CA by distinguishing the most important morphological characters responsible for the distinction of lateral branches.

Discussion

Thucydia mahoningensis is represented by up to three orders of interconnected branches. Organic connection between the stem and lateral branching systems suggests a growth pattern similar to that of juvenile trees of *A. heterophylla* (figs. 2A) and related species. Here, an orthotropic stem bears series of pseudo-whorls of lateral plagiotropic branches (figs. 2A-B). Orthotropic stems with lateral plagiotropic branches, like those of *A. heterophylla*, have been proposed as the basic architectural model for primitive walchian conifers (Florin 1938-1945, 1951; Hernandez-Castillo et al. 2003). Cluster and principal components analyses yield similar results, but because of the PCA character correlation, we know what morphological variables are important in differentiating lateral branches of *Thucydia*. Two main sets of specimens are recognized among the fossil branches (figs. 2, 3). In both cases, specimen G8 seems to be entirely different from the rest of the specimens, and it is characterized by an extremely large diameter of the penultimate stem. Specimens G1 and G190 are more similar to each other than the rest of the branches. The same pattern is observed for other clusters such as G25-G27, Gm2-G205, and G15-G16. Specimens G15 and G16 (fig. 2A) are counterparts of the same specimen, where measurements were taken from different ultimate shoots. Cluster analysis confirms that these specimens have the same characteristics. By contrast, differences were found when a principal components analysis was performed (fig 2B), even though they are different views of the same specimen. This confirms previous observations (Hernandez-Castillo et al. 2001) that different views of the same branch (due to splitting of the rock and/or preservation) may have an impact on the morphological features displayed by fossil conifer specimens.

Cluster analysis displays a hierarchical distribution of specimens but it is unable to explain differences between specimens G15 and G16. Principal components analysis displays a three dimensional distribution of the fossil branches, and it also explains distributions in terms of the characters used in the analysis. Distribution of fossil lateral plagiotropic branching systems can be correlated to specific morphological characters of the first, second and third components respectively (table 3). Cluster "a" is characterized by lateral plagiotropic branching systems that have small number and size of penultimate and ultimate shoots with large insertion angles of leaves at apical region (A2A) of ultimate shoots. Cluster "b" is characterized by large lateral branches with long ultimate shoots and small insertion angles (A2B) of leaves at the base of ultimate shoots.

Both clusters "a" and "b" also correspond to previously described branching shapes in *Thucydia mahoningensis* (Hernandez-Castillo et al. 2001). Small lateral plagiotropic branches shown in specimens defining cluster "a" display a deltoid shape, while larger branching systems of cluster "b" correspond to ovoid branches. Consequently, characters that explain most of the variation in the first three components can be used to identify and differentiate among the lateral branches of this primitive conifer.

Thucydia mahoningensis produced an orthotropic monopodial stem with regular tiers of vegetative plagiotropic branches that bear well-developed ultimate shoots (Hernandez-Castillo et al. 2003). Trees with a monopodial stem and series of regular plagiotropic branches conform to Massart's model of tree architecture (Hallé and Oldeman 1970; Hallé et al. 1978). These include both *T. mahoningensis* and *A. heterophylla* (Veillon 1978; Hernandez-Castillo et al. 2003). Characters found with principal components analysis help to differentiate basic shapes of lateral branches in *T. mahoningensis*. Such shapes are also found in *A. heterophylla* where small, deltoid branches (e.g., fig. 1F) are usually found near the apex of young trees, while larger branches (e.g., fig. 1E) commonly occur at intermediate and basal regions of such trees (Hernandez-Castillo et al. 2003). Because these characters are useful for differentiating among fossil lateral branches, they may be helpful for differentiating among branches of *A. heterophylla* as well. Therefore, a detailed analysis of the ranges of variation of *A. heterophylla* may produce a tree architecture and growth model that can be used to correlate and compare primitive conifer remains.

Tables

Table 2.1-1. List of characters used in multivariate analyses of lateral plagiotropic branching systems of *Thucydia mahoningensis*.

Characters	
Diameter of penultimate shoot at basal region	**DPB**
Diameter of penultimate shoot at apical region	**DPA**
Length of penultimate shoot	**LPS**
Diameter of ultimate stem at base of stem (mean)	**DUB**
Diameter of ultimate stem at apex (mean)	**DUA**
Number of ultimate shoots per penultimate shoot	**NUS**
Length of leaves at proximal region of ultimate shoots (mean)	**LBU**
Length of leaves at distal region of ultimate shoots (mean)	**LAU**
Thickness of leaves at proximal region of ultimate shoot (mean)	**TBU**
Thickness of leaves at distal region of ultimate shoot (mean)	**TAU**
Angle 1 on leaves at proximal region of ultimate shoot (mean)	**A1B**
Angle 1 on leaves at distal region of ultimate shoot (mean)	**A1A**
Angle 2 on leaves at proximal region of ultimate shoot (mean)	**A2B**
Angle 2 on leaves at distal region of ultimate shoot (mean)	**A2A**

Table 2.2-2. Eigenvalues and variance of principal components analysis of lateral branches of *Thucydia mahoningensis.*

PCA	**Eigenvalue**	**Percent**	**Cumulative**
1	4.763	34.023	34.023
2	2.730	19.505	53.529
3	2.023	14.452	67.981

Table 2.1-3. Principal components analysis eigenvectors of lateral branches of *Thucydia mahoningensis*.

Character	PC 1	Character	PC 2	Character	PC 3
DPB	0.772	DPB	0.289	DPB	-0.433
DPA	0.627	DPA	0.737	DPA	-0.14
LPS	0.636	LPS	0.313	LPS	-0.526
DUB	0.098	DUB	0.341	DUB	-0.383
DUA	0.396	DUA	-0.83	DUA	-0.155
NUS	0.505	NUS	-0.425	NUS	-0.477
LBU	0.718	LBU	0.218	LBU	0.464
LAU	0.535	LAU	0.252	LAU	0.41
TBU	-0.368	TBU	0.292	TBU	0.357
TAU	-0.406	TAU	0.396	TAU	0.301
A1B	-0.269	A1B	0.491	A1B	-0.47
A1A	-0.307	A1A	0.473	A1A	0.09
A2B	-0.705	A2B	0.021	A2B	-0.601
A2A	-0.91	A2A	0.116	A2A	-0.302

Figure Captions

Figure 1. *Thucydia mahoningensis* Hernandez-Castillo, Rothwell & Mapes vegetative shoots. Figure 1A. Line drawing from specimen OUPH 13411 showing orthotropic stem with lateral plagiotropic branches attached to it. OUPH 13411 (G200), scale = 1 cm. Figure 1B. Large plagiotropic branching system showing overall ovate shape, and insertion angles, size, and number ultimate shoots. OUPH 13412, scale = 10 cm. Figure 1C. Medium size plagiotropic branching system displaying overall deltoid shape, size and insertion angles of ultimate shoots. OUPH 13413 (G8), scale = 2.5 cm. Figures 1D to 1F. Young tree of *Araucaria heterophylla* (Salisb.) Franco, Ohio University, Athens, Ohio. Figure 1D. Third node from apex to base showing an orthotropic antepenultimate stem with lateral plagiotropic branches. Note different size of antepenultimate, penultimate leaves, and ultimate leaves. Scale = 1 cm. Figure 1E. Ovate lateral plagiotropic branching system showing overall shape. Scale = 10 cm. Figure 1F. Deltoid plagiotropic lateral branching system showing overall shape, angles of insertion of ultimate shoots. Scale = 10 cm. Figure G. Line drawings of an deltoid lateral plagiotropic branching systems. Figure H. Line drawing of ovate lateral plagiotropic branching system.

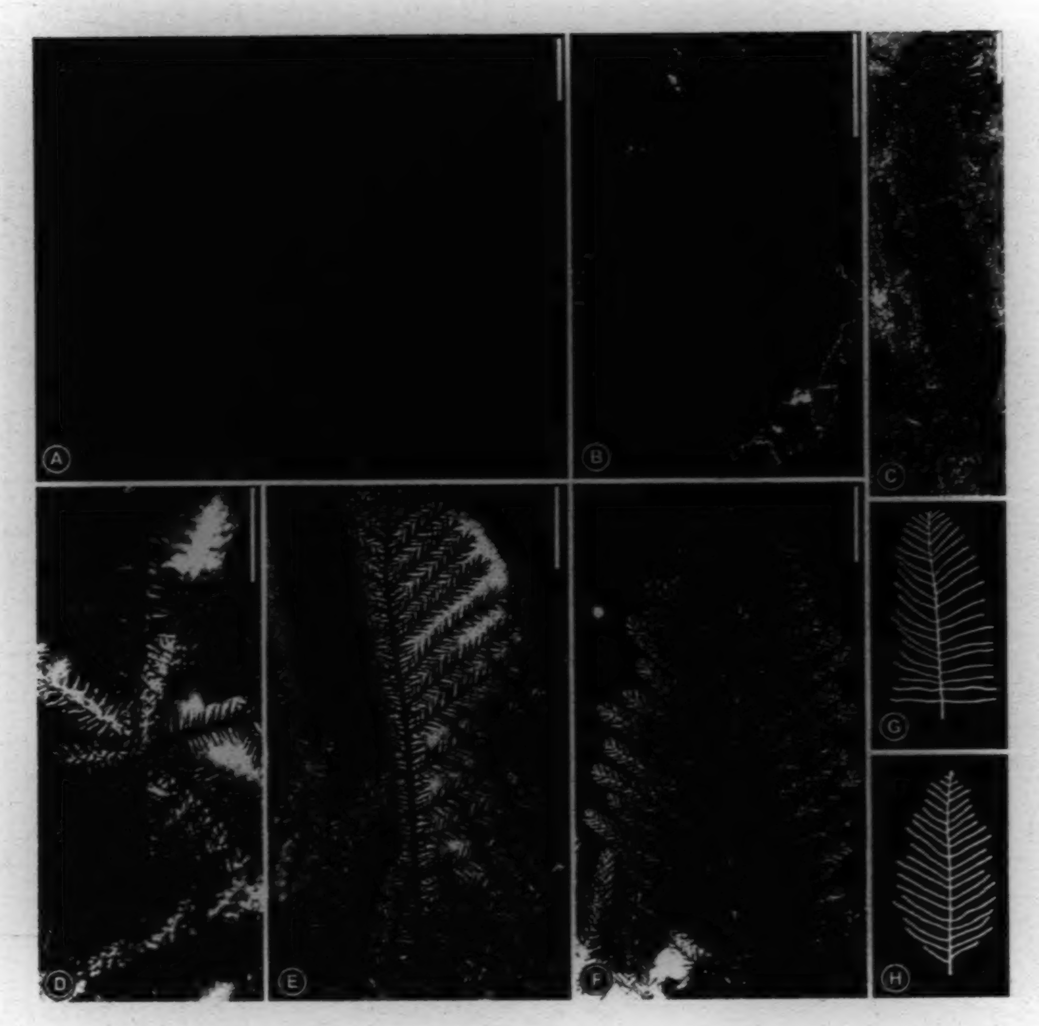
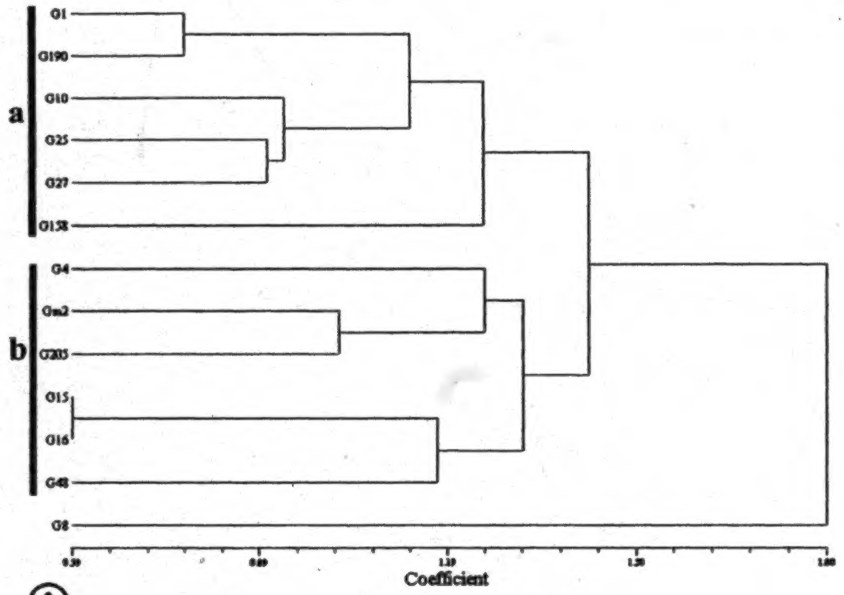
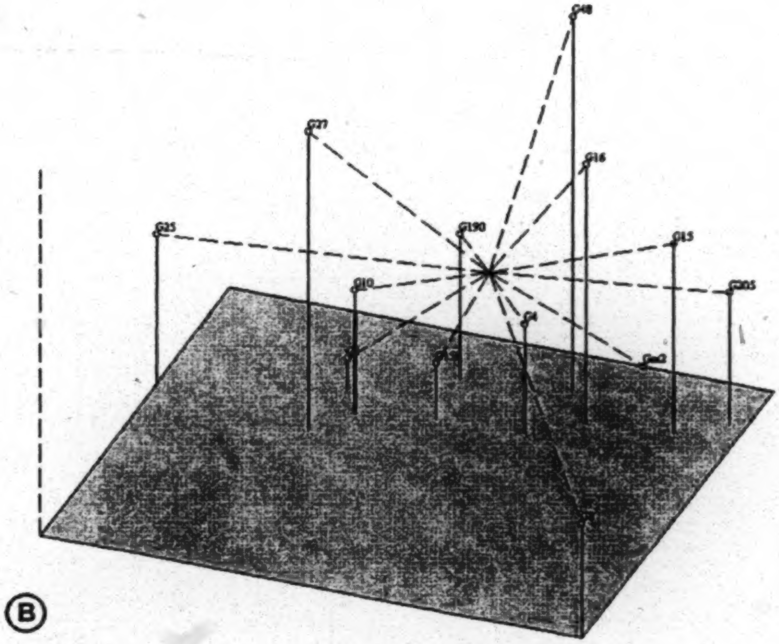

A
B
C
D
E
F
G
H

Figure 2. Multivariate analysis of lateral plagiotropic branching systems of *Thucydia mahoningensis*. Figure 2A. Phenogram showing results of cluster analysis. Note position of specimen G8 and distribution of two main clusters. Figure 2B. Three dimensional graph of principal components analysis. Note disposition of specimens on X, Y, and Z axes. Note distribution of two main groups of specimens to the left ("a") and to the right ("b"). Also note location of specimens G25 (far left side) and G8 (far right corner).

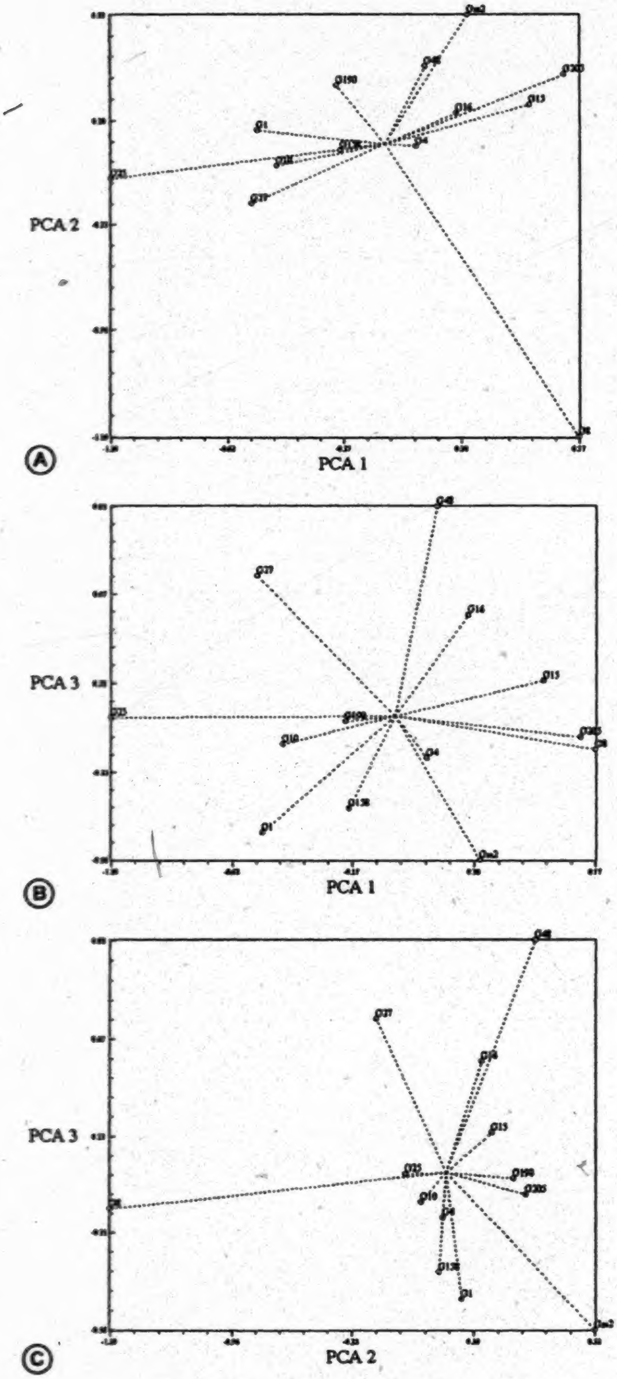

a
b
G1
G190
G10
G25
G27
G158
G4
Gm2
G205
G15
G16
G48
G8
0.30
0.68
1.05
1.43
1.80
Coefficient

Ⓐ


G48
G27
G16
G190
G25
G15
G10
G205
G4
Gm2

Ⓑ

Figure 3. Two dimensional graphs of principal components analysis of lateral plagiotropic branching systems of *Thucydia mahoningensis* Figure 3A. First and second components, note clusters of specimens to the left ("a") and to the right ("b"), and location of specimen G8. Figure 3B. First and third components, note clusters "a" and "b". Figure 3C. Second and third components, note distribution of clusters "a" (left) and "b" (right), and specimens G8, G48 and Gm2.


PCA 2
PCA 1
Ⓐ
g190
g1
g27
g15
g16
PCA 3
PCA 1
Ⓑ
g27
g14
g15
g10
g4
g138
g1
PCA 3
PCA 2
Ⓒ
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g15
g25
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g205
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g4
g138
g1

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Chapter 2.2

Identification of walchian conifers using a multivariate approach

Introduction

The most primitive conifers from the Upper Carboniferous of Euramerica are usually preserved as coalified compressions/impressions of lateral branches and cones that display morphological and cuticular features (Florin 1938-1945, 1950; Clement-Westerhof 1984; Kerp et al. 1990; Mapes and Rothwell 1984, 1991; Kerp and Clement-Westerhof 1991; Meyen, 1997; Hernandez-Castillo et al. 2001). Current descriptions of most of these taxa rely heavily on morphological and cuticular characters of leaves such as size, shape, angles of divergence, and stomatal distribution (Hernandez-Castillo et al. 2001). However, ranges of variation in leaves are either overlapping or unknown for nearly all previously described species (Hernandez-Castillo 2000; Hernandez-Castillo et al. 2001, 2003), and cuticles on vegetative and reproductive organs in an individual conifer plant can differ markedly (Hernandez-Castillo et al. 2001). Thus, current methodology for identifying species of primitive conifers is often unreliable and confusing.

Previous multivariate analyses using Thucydia mahoningensis Hernandez-Castillo, Rothwell and Mapes distinguished two basic types of lateral branches that have been compared to lateral branches of living Araucaria heterophylla (Salisb.) Franco (Hernandez-Castillo et al. 2002; 2003). Therefore, a detailed analysis of the ranges of variation in A. heterophylla is needed to produce a tree architecture and growth model that can be used to correlate and compare primitive conifer remains. However, individual measurements and ranges of variation in lateral branches of living Araucaria species and most fossil species were unknown. Here, I analyze and compare ranges of variation within a single unequivocal primitive conifer species, T. mahoningensis, to previously described fossil conifer species from Euramerica and extant A. heterophylla by means of multivariate analyses. This is the first multivariate analysis that includes a large data set (25 taxa). The goal was to test if these ranges can be used to a) identify patterns among conifer branches in the fossil record, and b) to accurately identify fossil conifer species in the Upper Carboniferous.

Materials and Methods

Specimens in this study include 13 of Thucydia mahoningensis (ThG) (Upper Carboniferous), 23 specimens of previously described conifers from Europe (Lower Permian), and 39 lateral branches of a single juvenile tree of Araucaria heterophylla (V1Br1-V8Br3, Table 1). Fossil specimens are preserved as coalified compressions/impressions. Specimens of Thucydia mahoningensis are from the 7-11 Mine locality in Columbiana County, Ohio, USA (McComas 1988; Hernandez-Castillo et al. 2001). European species were described by Florin (1938-45) from Lower Permian of the Czech Republic, France, and Germany (Table 1). Lateral branches of A. heterophylla were collected from trees donated from a nursery in Woonona, New South Wales, Australia. Fossil specimens are housed at the Ohio University Paleobotanical Herbarium, Athens, OH, USA, while specimens described by Florin (1938-45) are housed at different institutions throughout Europe (Table 1).

Branches of A. heterophylla were collected from each node or verticill (V) of a juvenile tree (1 m high), from the apex (V1) to the base of the tree (V8). These branches were coded using the verticill and branch number (e.g., V1Br1= verticill one, branch one). Museums were abbreviated in the following manner: Berlin = Museum für Naturkunde, Berlin; Dresden = Staatliches Museum für Mineralogie und Geologie, Dresden; Gotha = Museum der Natur, Gotha; Montpellier = Université de Montpellier II, Montpellier; Paris

= Muséum National d'Histoire Naturelle, Paris; Schleusingen = Naturhistorisches Museum Schloss Bertholdsburg, Schleusingen; Stockholm = Naturhistoriska Riksmuseet, Stockholm; Wien = Naturhistorisches Museum Wien, Vienna.

Specimens were digitized using a Nikon Coolpix 4300 digital camera. Images were stored as PSD and JPG files and measured with Image J, ver 1.33u (Rasband 2005). Fourteen characters were recorded for each branching system (Table 2), and ultimate shoots were measured on both sides of penultimate shoots (Hernandez-Castillo 2000). Five ultimate shoots were scored per specimen. Measurements of the distal regions were recorded one centimeter below the apex of the shoot to avoid inclusion of immature leaves. Araucaria heterophylla branches were numbered, removed, photographed, and measured with the same methodology as fossil specimens.

Cluster (CA) and Principal Components Analyses (PCA) were performed. Basic data matrices of fossil and living specimens were created in Excel and multivariate analyses performed in PC-ORD ver 4.0 for Windows (McCune and Mefford 1999). Cluster analysis was performed by calculating a similarity matrix between specimens using the Euclidian Distance Coefficient, and Group Average Linkage method (Sneath and Sokal 1973). Principal components analyses were performed with correlation matrices calculated with variance/covariance correlation index (McCune and Mefford 1999).

Results

Results of PCA are presented as individual and combined analyses. Individual analyses include A. heterophylla and previously described European species. Combined analyses include T. mahoningensis, Florin species, and A. heterophylla. Graphs include the first (Axis 1) and second (Axis 2) components (Fig. 1) except for the combined analysis where the first three components are shown (Fig. 2), and the first component vs. rank were plotted (Fig. 4). Cluster analyses are shown for the combined analysis (Fig. 3). Variance extracted from the first three components (Table 3) and the most highly correlated variables to each of the first three components are also presented (Table 4).

Araucaria heterophylla

Principal components analysis of all lateral branches shows seven groups of lateral branches (Fig. 1A). Branches may be of three categories: large, medium, and small based on their size. The correlation also implies a position on the tree. Apical and most basal branches are small in size, intermediate branches are large to medium, and branches either near the basal or apical regions are of medium size (Fig. 1A). The first three components account for 96.79 % of the variation (Table 3) and may reach 99% when the fourth component is included. The most highly correlated character associated with the first component is the length of penultimate shoots (LPS), while the second component is correlated to angles of leaf divergence A1A and A2A (Table 4). The third component is associated with angles of leaf divergence A1B and A2B (Table 4).

European species

Principal components analysis of previously described European species shows three clusters of species that include E. filiciforme, German specimens of L. piniformis and miscellaneous specimens of Lebachia from France (Fig. 1B). Isolated specimens include two E. filiciforme branches from Germany and France, and one L. piniformis branch from Germany (Fig. 1B). The first three components account for 96.79 % of the variation (Table 3). The most highly correlated characters associated with the first component are thickness of proximal leaves on ultimate shoot (TBU) and angles of leaf divergence A1A and A2B (Table 4). The second component is correlated with the number of ultimate shoots (NUS) while the third component is associated with length of proximal leaves on ultimate shoots (LBU), and length of penultimate shoots (LPS).

Combined analyses with fossil taxa and A. heterophylla

Principal components analysis of all extinct and extant taxa shows five clusters where E. filiciforme, L. piniformis, Montpellier taxa, T. mahoningensis, and A. heterophylla can be distinguished (Figs. 2A-B). The first two components show a clear cluster differentiation between all taxa. First and third components, however, show an overlap between L. piniformis and Montpellier taxa (Fig. 2B). In both graphs, A. heterophylla is characterized by the same seven clusters as before (Fig. 1A). The first three components account for 96.79 % of the variation (Table 3). The most highly correlated character associated with the first component is penultimate shoot length (LPS). The second component is correlated with thickness of leaves near the base of ultimate shoots (TBU) and angles of leaf divergence A1A and A2A (Table 4). The third component is associated with angles of leaf divergence A1B and A2B, and number of ultimate shoots per branch (Table 4). When the first component is plotted against the rank, a trend in the distribution of the specimens based on size and position of their lateral branches is clearly seen (Fig. 3). No definite size to shape branch clusters were observed within the European specimens. Thucydia mahoningensis is the only fossil taxon that shows at least three main clusters of branches (Fig. 3).

Cluster analysis basically shows the same clustering found with PCA (Fig. 3). Two main clusters distinguish A. heterophylla from all fossil taxa. This extant conifer comprises two clusters: one containing most branches (small to medium, apical, basal, and nearly apical and basal) and a second one that only includes large intermediate-sized branches (Fig. 3). Fossil taxa are grouped in two main clusters, one with Thucydia "a" branches (small deltoid) and a major cluster with Thucydia "b" branches (large ovoid), L. piniformis, Montpellier taxa, and E. filiciforme (Fig. 3).

Discussion

This multivariate approach provides another method for identifying diagnostic characters of lateral branches in primitive conifers. Principal component analyses using fourteen characters was able to differentiate branches of living A. heterophylla and can be correlated to each node on the tree based on the length of penultimate shoot (LPS) and angles of divergence of leaves on ultimate shoots (A1A, A2A, A1B and A2B). Branch categories based on these characters are: small apical, medium near apex, medium intermediate, large intermediate, medium near base, and small basal. When European fossils were used in the analysis, it was possible to differentiate between E. filiciforme, L. piniformis and specimens from Montpellier, France (Table 1). This separation of European specimens suggests that at least the most typical species of walchian conifers can be differentiated using this approach. However, when analyses were done adding more Lebachioid taxa and removing E. filiciforme, most of these specimens did not show clear clusterings. Thus the inclusion of a contrasting taxon such as Ernestiodendron helps to emphasize the differences among lebachioid taxa.

Combined analyses of fossil taxa and A. heterophylla suggests the fourteen characters used here are useful in differentiating and correlating branching systems of conifers that follow Massart's tree architectural model (Veillon 1978). When all taxa are included, A. heterophylla maintains a definite position and produces clusters of branches that are organized by their size, shape, and position on the juvenile tree. These clusters are distinctly separated from any fossil taxa. Both T. mahoningensis and L. piniformis appear to show minor clusters of specimens that reflect different branch categories. These clusters of fossil specimens are due to the sample size and preservation quality of the specimens. Moreover, the distribution of these clusters suggests that most lateral branches of L. piniformis conform to a similar category of branches. In contrast, T. mahoningensis has a more distinguishable size and shape branching pattern, though it is not as clear as that exhibited in A. heterophylla. This pattern based on the size and shape implies definite positions on the tree. However, this pattern is not decipherable in most fossil taxa (Fig. 4).

These results show that even though taxa can be differentiated, no branching patterns can be accurately observed among fossil taxa. The species with the greatest variety of lateral branch specimens (T. mahoningensis) is the most clearly delimited of the fossils in this analysis, suggesting again a similar growth architecture to that of living araucarians (Hernandez-Castillo et al. 2003). The multivariate analysis done here involved more characters (14) and species (25) than any previous study (Bertholon 1996), suggesting that multivariate analysis of this kind can aid in differentiating species of fossil conifers. However, they are limited by the preservation and number of specimens available.

This multivariate analyses indicates that German L. piniformis specimens can be accurately differentiated from Thucydia, Ernestiodendron, and French lebachioid species. While discrete clusters of fossil species are present, individual specimens do not cluster in a manner equivalent to that found in Araucaria, where size, shape and position governs the orders of branching. Thus, additional types of branches (small apical and basal) need to be scored before using this methodology in a larger context to reconstruct fossil conifers. Caution should be taken that these analyses should be combined with reliable organ correlations to avoid confusion between clusters formed by taxa and clusters of branches from closely related species. These results reinforce the idea that orthotropic stems with lateral plagiotropic branches, like those of A. heterophylla, are the basic architectural model for primitive Euramerican walchian conifers (Florin 1938-1945, 1951; Hernandez-Castillo et al. 2003; Lausberg 2002).

Tables

Table 2.2-1. List of characters used in the multivariate analyses.

Characters	Code
Diameter of penultimate shoot at base	DPB
Diameter of penultimate shoot at apex	DPA
Length of penultimate shoot	LPS
Diameter of ultimate stem at base of stem (mean)	DUB
Diameter of ultimate stem at apex (mean)	DUA
Number of ultimate shoots per penultimate shoot (branch)	NUS
Length of leaves at proximal region on ultimate shoots (mean)	LBU
Length of leaves at distal region on ultimate shoots (mean)	LAU
Thickness of leaves at proximal region of ultimate shoot	TBU
Thickness of leaves at distal region of ultimate shoot (mean)	TAU
Angle 1 on leaves at proximal region of ultimate shoot	A1B
Angle 1 on leaves at distal region of ultimate shoot	A1A
Angle 2 on leaves at proximal region of ultimate shoot	A2B
Angle 2 on leaves at distal region of ultimate shoot (mean)	A2A

Table 2.2-2. List of specimens used in the analyses.

Data sets	Specimens
T. mahoningensis	ThG1, ThG4, ThG10, ThG15, ThG16, ThGm2,ThG8, ThG48, ThG25, ThG27, ThG205, ThG190,ThG158
A. heterophylla	V1Br1, V1Br2, V1Br3, V1Br4, V1Br5
	V2Br1, V2Br2, V2Br3, V2Br4, V2Br5
	V3Br1, V3Br2, V3Br3, V3Br4, V3Br5
	V4Br1, V4Br2, V4Br3, V4Br4, V4Br5
	V5Br1, V5Br2, V5Br3, V5Br4, V5Br5
	V6Br1, V6Br2, V6Br3, V6Br4, V6Br5, V6Br6, V6Br7
	V7Br1, V7Br2, V7Br3, V7Br4
	V8Br1, V8Br2, V8Br3
European specimens	FLP1 - *Lebachia piniformis* (Schloth.) Florin. Nonweiler, Saar-Nahe, Germany.Wien.
	FLP 2 - *Lebachia piniformis* (Schloth.) Florin. Gube Rummelbach, Lebach Saar, Germany. Berlin.
	FLP 3 - *Lebachia piniformis* (Schloth.) Florin. Berschweiler, Kirn-Nahe, Germany. Stockholm
	FLP 4 - *Lebachia piniformis* (Schloth.) Florin, Kehrwald, Niederwörresbach-Nahe, Germany. Dresden.
	FLP5 - *Lebachia piniformis* (Schloth.) Florin. Schwarzenbach, Saar-Nahe, Germany. Berlin.
	FLP6 - *Lebachia piniformis* (Schloth.) Florin. Thüringer Wald, Gottlob b. Friedrichroda, Germany. Gotha.
	FLP7 - *Lebachia piniformis* (Schloth.) Florin. Gottlob b. Friedrichroda, Germany. Schleusingen.
	FLP8 - *Lebachia piniformis* (Schloth.) Florin. Glasbach b. Klein-Schmalkkalden, Germany. Schleusingen.
	FLP9 - *Lebachia piniformis* (Schloth.) Florin. Glasbach b. Klein-Schmalkkalden, Germany. Schleusingen.
	FLP10 - *Lebachia piniformis* (Schloth.) Florin. Sudetengau, Otoviče, Czech Republic. Gotha.
	FLP11 - *Lebachia piniformis* (Schloth.) Florin. Lodève, France. Paris.
	FLP12 - *Lebachia piniformis* (Schloth.) Florin. Lodève, France. Dresden.
	FML1 - *Lebachia piniformis* (Schloth.) Florin. Lodève, France. Montpellier.
	FML2 - *Walchia*(*Lebachia*?) *schlotheimii* (Brogniart) Florin. Lodève, France. Montpellier.
	FML3 - *Walchia*(*Lebachia*?) *bertrandii* Florin. Lodève, France. Montpellier.
	FML4 - *Walchia*(*Lebachia*?) *bertrandii* Florin. Lodève, France. Montpellier.
	FEFB - *Ernestiodendron filiciforme* Florin. Saar-Nahe, Germany. Berlin Spandau.
	FEFB1 - *Ernestiodendron filiciforme* Florin. Thüringer Wald, Streitgern, b. Klein- Schmalkalden. Germany. Berlin.
	FEFB2 - *Ernestiodendron filiciforme* Florin. Nonweiler, Saar-Nahe-Gebiet. Germany. Wien.
	FEFB3 - *Ernestiodendron filiciforme* Florin. Thüringer Wald, Gottlob b. Friedrichroda, Germany. Stockholm.
	FEFB4 - *Ernestiodendron filiciforme* Florin. Thüringer Wald, Gottlob b. Friedrichroda, Germany. Gotha.
	FEFB5 - *Ernestiodendron filiciforme* Florin. Lodève, France. Paris.
	FEFB6 - *Ernestiodendron filiciforme* Florin. Lodève, France. Nancy.

Table 2.2-3. Variance extracted from the first three components.

Data set	**Axis**	**Variance (%)**	**Cumulative Variance (%)**
	1	50.931	50.931
Thucydia mahoningensis	2	42.304	93.235
	3	5.174	98.409
	1	96.42	96.42
Araucaria heterophylla	2	2.134	98.554
	3	0.921	99.475
	1	81.69	81.69
Florin specimens	2	12.63	94.321
	3	2.475	96.796
	1	89.882	89.882
T. mahoningensis + European specimens +	2	4.422	94.304
A. heterophylla	3	3.237	97.541

Table 2.2-4. Most important variables correlated to the first three components.

Data set	**Component**		
	1	**2**	**3**
Thucydia mahoningensis	LPS (-)	DPA (+)	NUS (-)
Araucaria heterophylla	LPS (-)	A1A (+)	A1B (+)
		A2A (+)	A1B (+)
European specimens	TBU,	NUS (-)	LBU (-)
	A1A (-)		LBU (-)
	A1B (-)		
T. mahoningensis + *A. heterophylla*	LPS (+)	A1B (+)	DPA (+)
		A2B (+)	LBU (+)
		NUS (-)	
European specimens + *A. heterophylla*	LPS (-)	NUS (-)	A1A (-)
		TBU (-)	A2A (-)
		A2B (+)	A1B (-)
T. mahoningensis + European specimens + *A. heterophylla*	LPS (+)	TBU (-)	A1B (-)
		A2A (-)	A2B (-)
		A1A (-)	NUS (+)

Figure Legends

Figure 1. A. Principal components analysis of lateral branches of Araucaria heterophylla showing taxa according to the first two components. Note size (small, medium, large) and position of branches (apex, intermediate, base). B. Principal component analysis of European specimens described by Florin. Note clusters of E. filicifome, L. piniformis and Montpellier specimens.

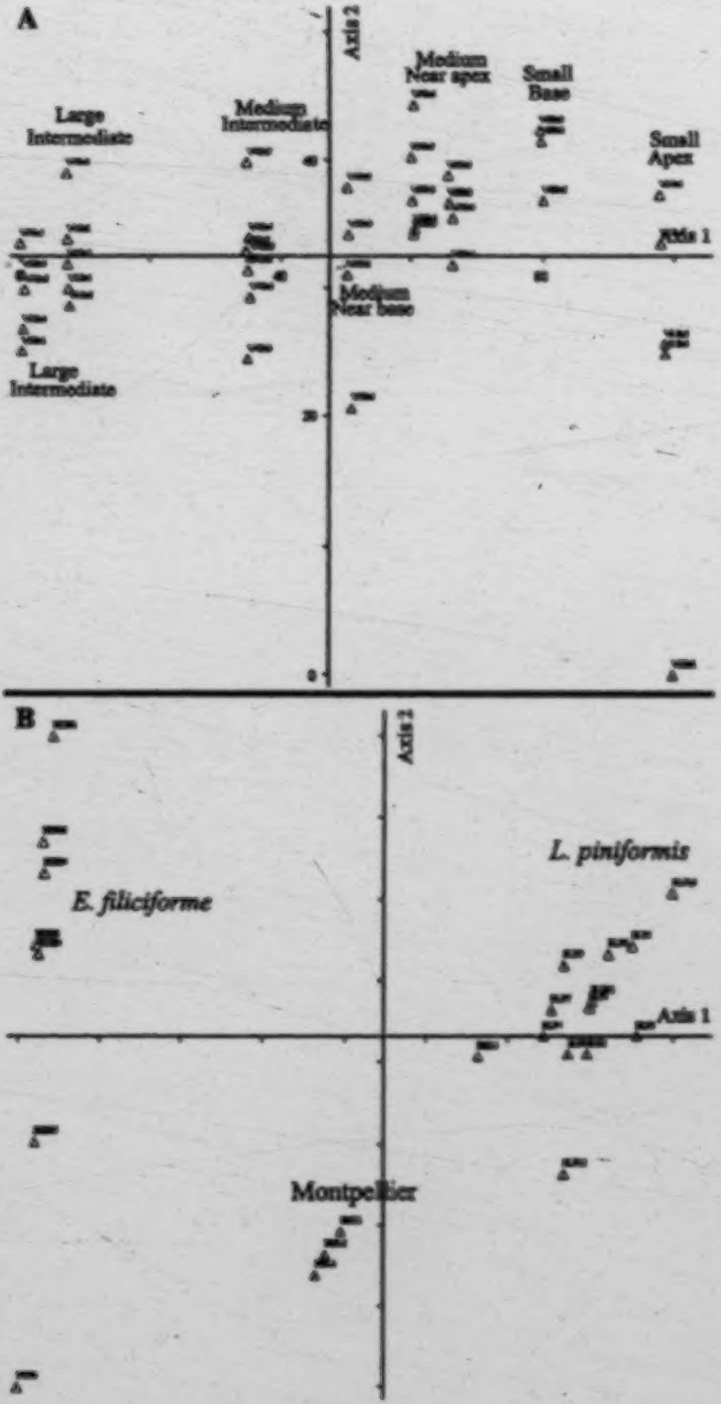

A
Axis 2
Medium
Near apex
Small
Base
Large
Intermediate
Medium
Intermediate
Small
Apex
Axis 1
Medium
Near base
Large
Intermediate
B
Axis 2
L. piniformis
E. filiciforme
Axis 1
Montpellier

Figure 2. Principal components analysis of *T. mahoningesis*, European specimens, and *A. heterophylla* using the first two components. Note species clustering and clusters of individual groups of lateral branches in *A. heterophylla*. B. Principal component analysis of *T. mahoningesis*, European specimens and *A. heterophylla*using the first and third components.

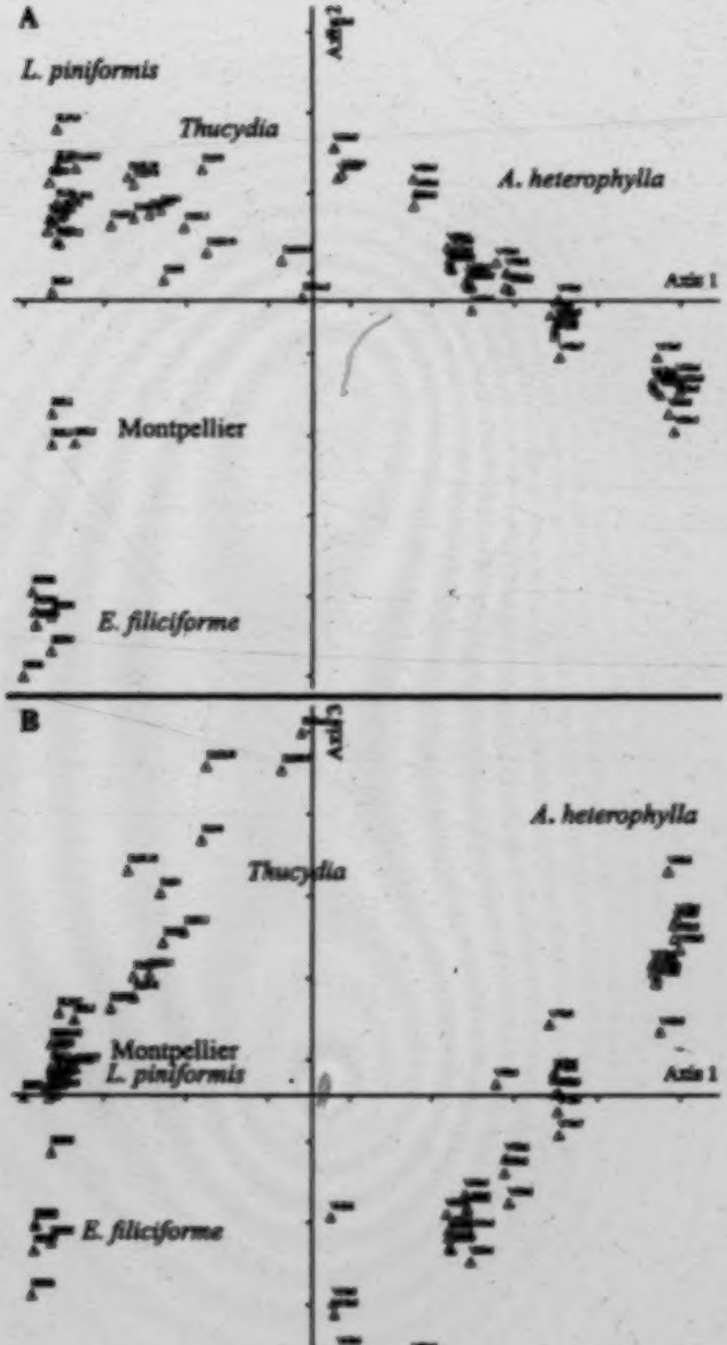

A
L. piniformis
Thucydia
A. heterophylla
Montpellier
E. filiciforme
Axis 2
Axis 1
B
A. heterophylla
Thucydia
Montpellier
L. piniformis
E. filiciforme
Axis 2
Axis 1

Figure 3. Cluster analysis of *T. mahoningesis*, European specimens and *A. heterophylla* using Euclidean distance. Note two main clusters with *A. heterophylla* and all fossils. Note seven categories of branches in *A. heterophylla*, two clusters in *T. mahoningensis*, and one cluster for both *E. filiciforme* and Montpellier specimens.

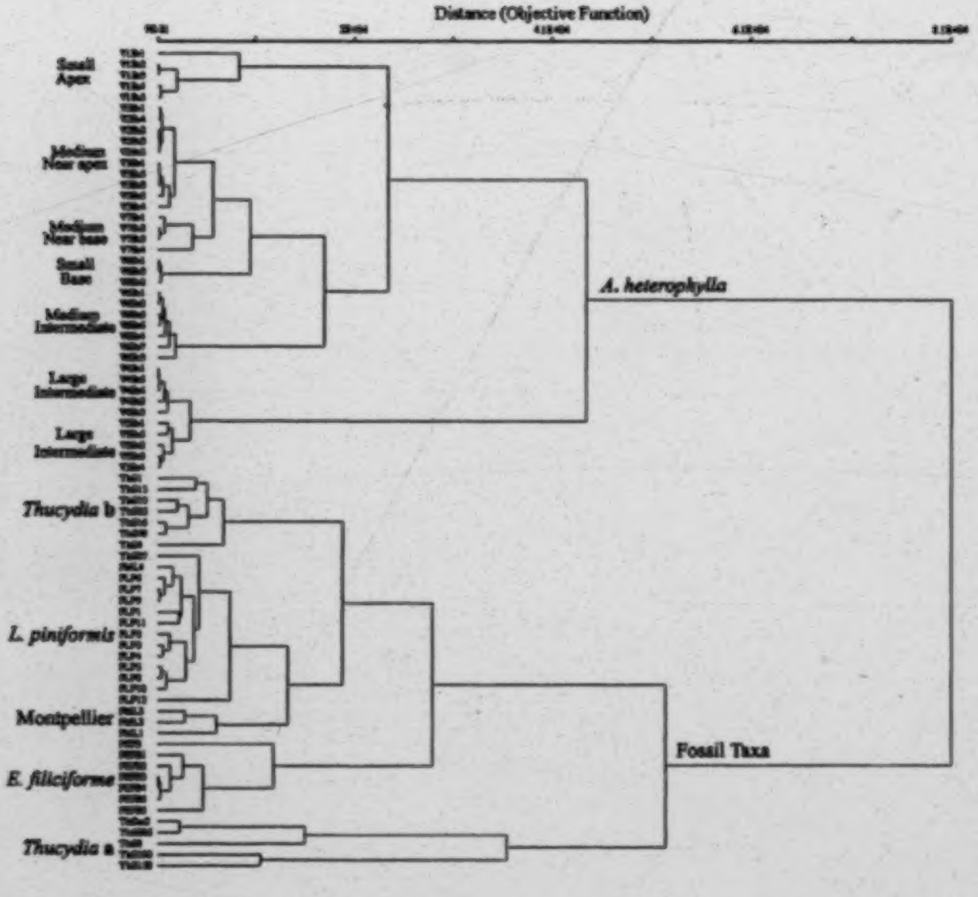
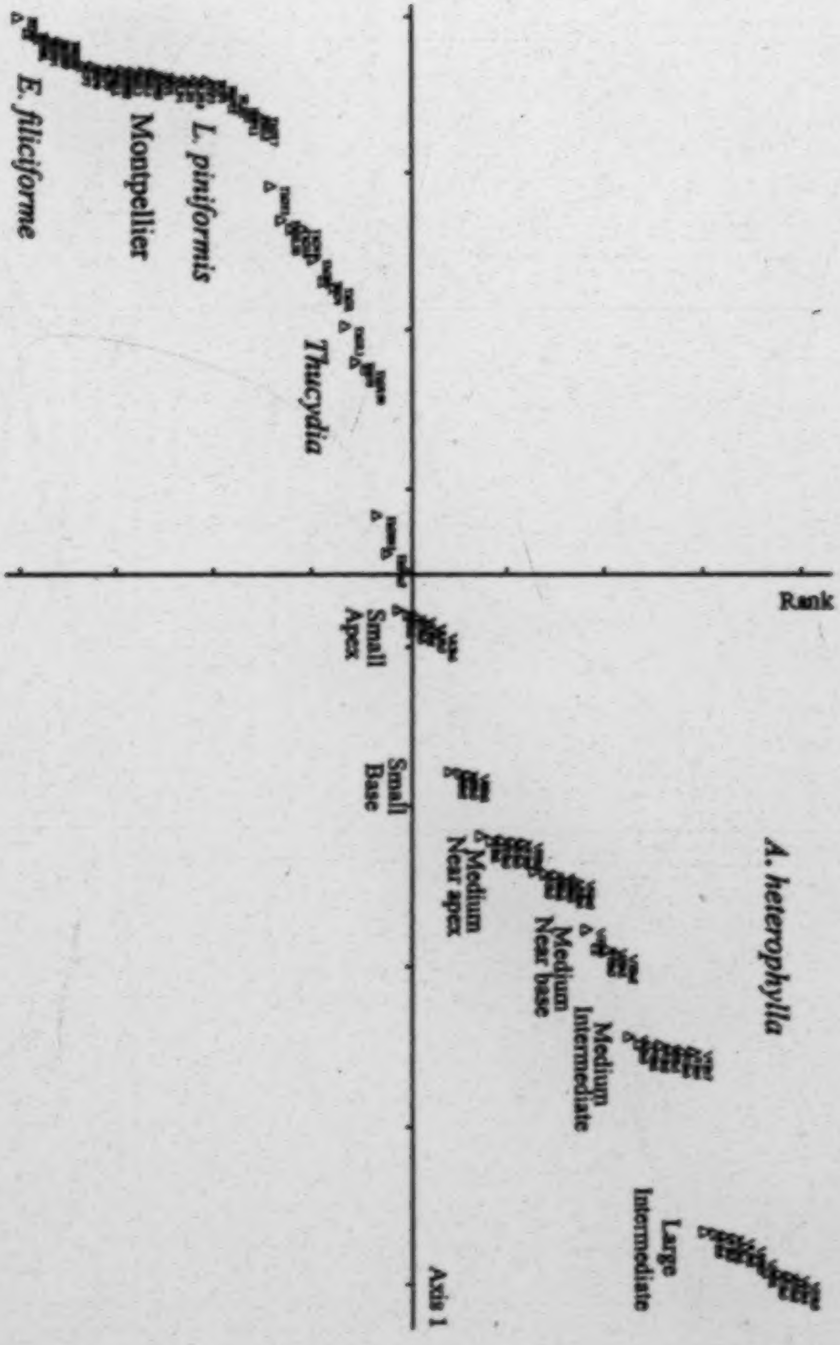

Distance (Objective Function)
Small Apex
Medium Near apex
Medium Near base
Small Base
Medium Intermediate
Large Intermediate
Large Intermediate
Thucydia b
L. piniformis
Montpellier
E. filiciforme
Thucydia a
A. heterophylla
Fossil Taxa

Figure 4. Principal component analysis of *T. mahoningesis*, European specimens and *A. heterophylla* showing first component vs. rank. Note main clusters of specimens. The first cluster includes *E. filiciforme*, Montpellier, and *L. piniformis*, the second *T. mahoningensis*, and the third *A. heterophylla*.


Axis 1
Rank
A. heterophylla
Large
Intermediate
Medium
Intermediate
Medium
Near base
Medium
Near apex
Small
Base
Small
Apex
Thucydia
L. piniformis
Montpellier
E. filiciforme

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CHAPTER 3

Whole plant reconstruction of *Emporia lockardii* and reevaluation of the Emporiaceae

Introduction

The fossil record of conifers can be traced back to the Upper Carboniferous (Pennsylvanian) and Early Permian of Europe and North America (Galtier et al., 1992; Rothwell et al., 1997). These Euramerican conifer species are commonly referred to as walchian conifers (Mapes and Rothwell, 1984), and they are classified in several families within the Voltziales (Florin, 1938-45; Visscher et al., 1986; Kerp et al., 1990; Mapes and Rothwell, 1991). The first systematic framework for walchian conifers was proposed by Florin in several different papers (1927, 1938-45, 1950, 1951). Florin's methodology uses a combination of morphological and cuticular characters of vegetative branches and cones to describe fossil conifer species. His monumental body of work on conifer systematics and the origin of ovulate cones in modern conifers has been broadly accepted, and to date his interpretations of both living and fossil conifers remain as some of the most influential (Florin, 1938-45, 1951).

However, more recent studies have challenged Florin's systematics and his interpretations of the most primitive conifers (Schweitzer 1963; Rothwell, 1982; Clement-Westerhof, 1984, 1987, 1988; Mapes and Rothwell, 1984, 1991, 1998; Meyen, 1984; Winston, 1984; Visscher, et al., 1986; Kerp, et al., 1990; Kerp and Clement-Westerhof, 1991; Hernandez-Castillo, et al., 2001a, 2001b, 2003; Rothwell et al., 2005). Most of these papers have been summarized previously (Hernandez-Castillo et al., 2001b), and a complete reevaluation and reexamination was proposed for these conifers employing new methodologies and reliable criteria for circumscribing species of walchian conifers as complete plants.

In the current study we employ this new approach in describing the whole plant reconstruction of *Emporia lockardii*. The reconstruction presented here is based on a combination of morphological, cuticular, and anatomical characters that correlate vegetative branches with pollen and ovulate cones. This paper is part of broader study to reinvestigate, describe, and reevaluate morphological characters and species of Euramerican Paleozoic walchian conifers. Our goal is to identify and reconstruct walchian conifer species as complete plants, so they can be used to resolve systematic relationships among fossil and living conifers.

Floristic analyses of the Hamilton Quarry have shown a conifer dominated flora derived from relatively dry basinal slopes (Mapes and Rothwell, 1988; DiMichelle and Aronson, 1992; Rothwell et al., 1997). Preservation of the fossil specimens allows for morphological, cuticular and anatomical analyses. Previous studies of the Hamilton Quarry flora include the first and most complete description of the internal anatomy of Paleozoic conifers and first evidence of inverted ovules (Mapes and Rothwell, 1984), origin of conifer seed dormancy (Mapes et al., 1989), first description of simple pollen cones with adaxial pollen sacs (Mapes and Rothwell, 1998), and the establishment of the family Emporiaceae (Mapes and Rothwell, 1991, 2003). It is the first locality where more than one conifer has been described as a whole plant (Rothwell and Mapes, 2001; Rothwell et al., 2005). *Emporia lockardii* Hernandez-Castillo, Stockey, Rothwell & Mapes is the third conifer reconstructed as a whole plant from this site making the Hamilton Quarry the only locality in the world where three conifer species are described as whole plants.

Materials and methods

The specimens used in this study are preserved as coalified compressions with preserved cuticles and cellular permineralizations. They occur in Late Pennsylvanian laminated carbonate mudstones of the Hartford Limestone, Topeka Limestone Formation, Shawnee Group, located east of Hamilton, Kansas, USA (Fig. 1; Mapes and Rothwell, 1984; Bridge, 1988; French et al., 1988; Busch et al., 1988). These beds represent channel deposits in an estuarian environment under tidal influence (French et al., 1988; Fahrer et al., 1990; Fahrer, 1991; Feldman et al., 1993). *Emporia lockardii* is represented by 85 specimens. Sixteen of these are plagiotropic leafy branching systems with penultimate and ultimate shoots attached (Figs. 2-7). Two have cuticles preserved and one is anatomically preserved. Fifty one are pollen cones, and six of these are attached to ultimate shoots; thirteen have cuticles preserved and sixteen are anatomically preserved. Eighteen are ovulate cones and most of them are attached to penultimate shoots with leaves. Eight of them are new to this study while the remaining ten cones were previously described in Mapes and Rothwell (1984). Five ovulate cones have cuticles and three are anatomically preserved.

Specimens were initially revealed on split surfaces of the limestones. Cuticles were macerated from the matrix with dilute (0.5-1%) HCl, rinsed in distilled water, bleached in Lysol toilet bowl cleaner (Reckitt Benckiser, Toronto, Canada), allowed to air dry on microscope slides, and mounted under a cover slip with Eukitt (O. Kindler GmbH Co., Freiburg, Germany). Cuticles for scanning electron microscopy were air dried on specimen stubs and coated with (100 Å) gold, and examined on a JEOL (Japan Electron Optics Ltd.) 6301 FXV and a Phillips XL30 ESEM (FEI Co., Tokyo, Japan) scanning electron microscopes. Some anatomically preserved specimens were prepared with the cellulose acetate peel technique (Joy et al., 1956), and others were cut into wafers and ground thin enough to transmit light. Compressed specimens with some anatomical preservation were etched with 1-5% HCl, flooded with acetone, and a cellulose acetate peel was placed on the split surface. These surface pulls were removed while the acetate was still plastic enough to be pressed relatively flat under a heavy weight. Light microscopy was conducted using Zeiss Ultraphot IIIB and WL microscopes, and images captured with a MicroLumina digital scanning camera (Leaf Systems Inc., Bedford, MA) or a PhotoPhase digital scanning camera (Phase One A/S, Frederiksberg, Denmark). Images were processed using Adobe Photoshop. All specimens are housed in the Ohio University Paleobotanical Herbarium, Athens, OH.

Results

***Systematics* -**

***Class* –** Coniferopsida

***Order* –** Voltziales

***Family* –** Emporiaceae Mapes et Rothwell

Genus – *Emporia* Mapes et Rothwell

***Species*: *Emporia lockardii* (Mapes et Rothwell) Mapes et Rothwell emend. Hernandez-Castillo, Stockey, Rothwell et Mapes (Figs. 1-50).**

Synonyms* – *Lebachia lockardii **G. Mapes et G. W. Rothwell, Palaeontology 27: 72. 1984. Plate 9, Fig.5, Plate 10, Fig. 1-3, 5, 6; Plate 11, Figs. 1, 3-6; Plate 12, Fig. 4; Plate 13, Figs. 1, 3, 5; Plate 14, Figs. 1-8.**

Emporia lockardii (G. Mapes et G. W. Rothwell) G. Mapes et G. W. Rothwell comb. nov., N. Jb. Geol. Paläont. Abh.,183: 277. 1991.

Emporia lockardii (G. Mapes et G. W. Rothwell) G. Mapes et G. W. Rothwell., Taxon 52:327. 2003.

Characters modified or added in the familial and generic diagnosis are written in bold face.

Emporiaceae emended diagnosis – Small eustelic coniferous trees with orthotropic stem, plagiotropic branches, and dense wood. Leaves helically arranged, simple on ultimate branches; **simple or** forked on penultimate shoots. Fertile organs consisting of simple pollen cones and compound ovulate cones. Pollen cone axis bearing helically arranged amphistomatic sporophylls with adaxial pollen sacs bearing eusaccate prepollen. Ovulate cones with helically arranged, bilateral, dwarf shoots bearing sterile scales attached on all sides of dwarf shoot axis, recurved sporophylls interspersed with sterile scales on side of dwarf shoot facing cone axis.

Emporia emended diagnosis – Characters of genus those of family. Endarch stele with **uniseriate and multiseriate** bordered pits on secondary xylem tracheids; rays 1-2 cells wide, resin rodlets in ground tissues. Leaves amphistomatic; adaxial surface with two long stomatal bands 2-12 stomatal complexes wide with some shared subsidiary cells, diminishing to single rows or scattered stomata near tip of small leaves; abaxial surface with two shorter basal bands, diminishing to narrow bands or scattered basal stomata. Stomata monocyclic and dicyclic with unipapillate subsidiary cells. Pollen cones cylindrical to elongated with herbaceous axis; sporophylls with narrow shank and keeled distal lamina; numerous pollen sacs attached to adaxial surface of sporophyll shank; prepollen monosaccate, monolete. Ovuliferous dwarf shoots with one or more narrow sporophylls recurved near apex, each bearing one inverted terminal ovule. Embryos polycotyledonary.

***Emporia lockardii* emended diagnosis –** Characters of species those of genus. Leaves on penultimate shoots simple to forked, narrowly triangular to linear (face view), slightly concave to S-shaped (side view), 8-10 mm long, 1-2 mm wide. Leaves on ultimate shoots narrow, sub- triangular to linear (face view), slightly concave to S-shaped (side view), 1.7-5.0 mm long, 0.4-1.16 mm wide. Epidermal cells rectangular, elongate to polygonal, often unipapillate; marginal trichomes present. Adaxial stomatal bands, two, separated by epidermal cells. Stomata 58 x 46 μm in diameter, 5-9 unipapillate subsidiary cells, guard cells sunken. Adaxial trichome bases few to none. Abaxial stomatal bands, two, short, narrow to individual rows. Abaxial trichome bases numerous. Secondary xylem tracheids uniseriate, biseriate, bordered pits circular; wood rays 1-8 cells high. Pollen cones cylindrical to ellipsoidal, 0.5-5.3 cm long, 0.5-2.1 cm wide; microsporophylls 0.25-5.0 mm long, 2-3 mm wide. Pollen sacs 8-14 per microsporophyll, adaxial, ellipsoidal, attached to a single area on shank. Distal lamina of microsporophyll with 2-4 adaxial stomatal bands; stomata 20 x 27 μm, 4-6 unipapillate subsidiary cells; epidermal cells unipapillate. Prepollen of *Potonieisporites* type, subcircular to bilateral in polar view, 87-127 μm wide, 64-106 μm long. Leaves on ultimate shoots subtending pollen cones like those on vegetative ultimate shoots. Ovulate cones cylindrical to ellipsoidal, 5.0 cm long, 1.5 cm wide. Bracts forked with cuticular features like those of forked leaves on penultimate shoots. Axillary ovuliferous dwarf shoots free to base. Sterile scales linear to widely obovate, apex mucronate to mucronulate, 14-30, 2.1-4.3 mm long, 1.3-1.8 mm wide, amphistomatic like leaves on ultimate shoots. Sporophylls narrow, 1-3, covered by numerous trichome bases. Ovules bilateral, flattened, winged; base rounded to subcordate; attachment scar basal to sub-lateral; nucellus free from integument to near chalaza; nucellar beak present; pollen chamber simple.

Holotype. Ovulate cone and subtending penultimate shoot designated by Mapes and Rothwell, Palaeontology 27: 72. 1984, illustrated in: Plate 9, Fig. 5, Plate 10, Fig. 1-3, 5, 6; Plate 11, Figs. 1, 3-6; Plate 12, Fig. 4; Plate 13, Figs. 1, 3, 5; Plate 14, Figs. 1-8.

Specimens studied. Lateral branches M 4023, M 1077, M 1108A, M 1028, M2325, M1206A (Figs. 2-7). Branches showing penultimate and leaves on ultimate shoots with cuticles M 1206A (Figs. 8,10), M 608 A (Fig. 9), M 897 (Figs. 11-14), M 1188 (Figs. 15, 17-19), M 2325 (Fig. 16). Pollen cones M 3998, M 998, M 3047, M 1823, M 2762, M 2906, M3047, M 2903 (Figs. 20-26). Vegetative leaves on ultimate shoots attached to pollen cones M 1823 (Figs. 27, 28). Pollen cone macerations and pollen M 2906 (Figs. 29-35). Anatomically preserved pollen cones M 196 (Figs. 36, 37), M 157 (Figs. 38-40). Ovulate cones M 608 A (Figs. 41, 43), M 2963 E (Fig. 42). Cuticular macerations of ovulate cone M 1625 (Figs. 44-51).

Collecting locality. Hamilton Quarry; NW quarter, sec. 5 and 8, T. 24 S., R. 12E., Virgil seven and a half foot quadrangle, Greenwood County, Kansas, U.S.A. (Fig. 1).

Stratigraphic occurrence and age. Hartford Limestone, Topeka Limestone Formation, Shawnee Group, Late Pennsylvanian.

Description

Lateral Branches—The specimens consist of two orders of branching with a penultimate shoot that bears several ultimate shoots with helically arranged leaves (Figs. 2-7). Most branches are plagiotropic (Figs. 2-4, 6-7) but a few show a slightly irregular branching (Fig. 5), most likely due to preservation. Branch shape ranges from ovoid to deltoid (Figs. 3-5, 6). The largest plagiotropic branch is 18 cm long and 7.5 cm wide (Fig. 4). The longest ultimate shoot (3.75 cm long) occurs in the midregion of the branch (Fig. 2) and the shortest (1 cm) on a small deltoid lateral branch (Fig. 6). Most lateral branches are broken at the very base or apex (Figs. 2-7), indicating that some plagiotropic shoots were larger than the specimens shown here. Penultimate shoots range from 1.0 to 4.0 mm wide from the apex to the base.

Leaves on penultimate shoots —Leaves are helically arranged, simple or forked when found on large branches or at the base of ovulate cones (Fig. 2-7, 8-10). They are 8-10 mm long and 1.0-2.1 mm wide. In face view, leaves on penultimate shoots range from narrowly triangular (Figs. 4-7, 11) to linear (Figs. 8, 12), and in side view they range from slightly concave (Figs. 4, 5) to slightly S-shaped (Figs. 6, 7). Leaves on penultimate shoots diverge at 26-83° angles from the stem (Table 1; Figs. 4-7).

Leaves are amphistomatic (Figs. 11-14) with two long adaxial bands of stomata that contain 2-5 stomata, separated by a stomatal free zone (Figs. 11, 12). Stomata are monocyclic, semicircular to ellipsoidal and have 6-8 subsidiary cells with small, erect papillae (Fig. 14). Stomata are separated by groups of epidermal cells that run along and across the stomatal band (Figs. 12, 14, at brackets). The stomatal free zone is composed of polygonal to rectangular epidermal cells (Fig. 12). Epidermal cells on marginal zones of the leaf and in stomatal free zones display few or no papillae (Fig. 16), and the margin of the leaf has short trichomes (Figs. 12, 13). The abaxial surface is covered completely by trichome bases (Table 1; Fig. 13).

Leaves on ultimate shoots —Leaves on ultimate shoots are helically arranged, simple, 1.7-5.0 mm long, and 0.4-1.1 mm wide (Table 1; Figs. 1-7, 9, 10, 15). Leaves on ultimate shoots may be narrow sub-triangular (Fig. 15) to linear in face view (Fig. 10), or slightly concave (Figs. 2-7) to slightly S-shaped in side view (Figs. 3, 5). Leaves diverge from the base of the shoot at 26-63° (Figs. 3, 4) and at 28-69° at the apex (Table 1; Fig. 6). Leaves are amphistomatic with two long bands of adaxial stomata (Fig. 15). Stomatal bands contain 2-5 stomata that run from the apex to the very base of the leaf, separated by a stomatal free zone (Figs. 15, 16). Leaf margins and stomatal free zones have rectangular epidermal cells that are elongated longitudinally with few or no papillae (Fig. 15, 16). Stomatal complexes are separated by groups of epidermal cells, some stomata may be in contact with each other, but subsidiary cells are not usually shared (Figs. 16, 17). Stomata are monocyclic, ellipsoidal, 58 x 46 μm, and have 5-9 papillate subsidiary cells (Figs. 16, 17). Papillae are thin, small and usually overarching (Fig. 17). The abaxial surface shows two short, narrow stomatal bands or individual rows of stomata (Figs. 18, 19). Short and narrow stomatal bands are often located at the base of the leaves and are 2-4 stomata wide. However, many leaves have rows of stomata that run along the entire abaxial surface of the leaf (Figs. 18, 19). These abaxial rows are commonly found in the central part of the leaf, but they may be located near the margins as well. Scattered abaxial stomata also may be found near the base of the leaf. The entire abaxial surface is covered by trichome bases (Table 1; Figs. 18, 19).

Pollen cones attached to ultimate shoots—Many pollen cones from the locality are attached to ultimate shoots that bear leaves (Figs. 20, 21, 25, 26, 27), but most of them are isolated and/or broken (Figs. 22, 23). Leaves on subtending ultimate shoots are 3-5 mm long and 1.6-2.2 mm wide. Leaf shape ranges from narrowly triangular to slightly elliptical (Table 1). Leaves have two bands of adaxial stomata separated by a stomatal free zone and epidermal cells with few or no papillae (Fig. 27). Stomatal bands contain 2-5 stomata and 5-7 papillate subsidiary cells, and stomata within these bands are separated from each other by groups of polygonal epidermal cells (Fig. 28).

Pollen cone morphology—Pollen cones are simple, terminal, cylindrical to ellipsoidal, 0.5-5.3 cm long, and 0.5-2.1 cm wide (Figs. 20-26). Cones bear helically arranged microsporophylls (Figs. 20-24), 0.25-5.0 mm long, and 2-3 mm wide with a narrowly triangular distal lamina (Figs. 20, 22, 23) and broad base (Figs. 22, 29). Microsporophylls have 2-4 bands of adaxial stomata (Fig. 29). Two main bands run along the entire distal lamina, and two short bands are usually found at the base of the lamina (Fig. 29). The main stomatal bands are separated by a stomatal free zone (Fig. 30). Stomata are monocyclic, 20 x 25 μm with 4-5 papillate subsidiary cells (Fig. 31). The microsporophyll is covered by epidermal cells with erect papillae (Figs. 29-31) and trichomes bases (Figs. 32-34). Trichome bases are circular and often broken showing a raised basal area and elongated epidermal cells surrounding the trichome base (Figs. 33, 34).

Pollen cone anatomy and prepollen—Mature (Figs. 20-24) and immature (Figs. 25, 26) pollen cones are present in the collection. Most mature cones show few pollen sacs with small amounts of pollen, while young cones are intact (Figs. 35-38). Longitudinal sections show a cone axis bearing helically arranged, peltate microsporophylls with a distal lamina that is at least three times larger than the heel (Figs. 36-38). Pollen sacs are abaxial, ellipsoidal and attached to a single area on the shank (Figs. 36-38). Eight to 14 pollen sacs have been found per microsporophyll (Figs. 36-39). Most pollen sacs are empty (Fig. 39) but some have prepollen grains that are semicircular with a single saccus surrounding a central body with a bent monolete suture and parallel folds (Fig. 40). Grains are 87-127 μm long, 64-106 wide μm and closely resemble *Potonieisporites neglectus* Potonié and Lele (Taggart and Ghavidel-Syooki, 1988) (Fig. 40).

Ovulate cones—Ovulate cones have been thoroughly described by Mapes and Rothwell elsewhere. However, two additional cones were macerated in this study and show a diversity in size and shape of sterile scales and sporophylls (Figs. 41-50). Compound cones are 5.0 cm long, 1.5 cm wide and cylindrical to ellipsoidal in shape (Figs. 41, 42). They are attached terminally to penultimate shoots with leaves (Fig. 41). The cone axis bears helically arranged bracts with axillary dwarf shoots that bear 14-30 sterile scales (Figs. 42, 43). Sterile scales range in shape from lanceolate (Fig. 43), to ellipsoidal (Fig. 44), to widely ovate (Fig. 45). Most sterile scales have short marginal trichomes (Figs. 43-45) and are 2.1 to 4.3 mm long, and 1.3 to 1.8 mm wide. Sporophylls are terminal, linear with a broad apex and upturned tip that shows a seed scar (Figs. 46, 47).

The epidermis of sterile scales is similar to that of leaves on ultimate shoots with two large adaxial bands of stomata separated by a stomatal free zone (Fig. 43). Stomatal bands can be distinguished by the presence of papillae on subsidiary cells (Figs. 48, 49). Individual stomata have 6-7 unipapillate subsidiary cells with a single erect or overarching papilla (Fig. 49). The abaxial surface is completely covered by trichome bases (Fig. 50).

Discussion

Emporia lockardii conforms to the general architecture recently determined for walchian conifers (Lausberg, 2002; Hernandez-Castillo et al., 2003; Rothwell et al., 2005). These are relatively small plants with determinate growth and plagiotropic lateral branches borne on orthotropic stems that produced terminal ovulate and pollen cones. *Emporia lockardii* (=*Lebachia lockardii*) was originally established to accommodate the first walchian conifer with a novel combination of characters derived from the morphology and anatomy of ovulate cones (Mapes and Rothwell, 1984). These novel characters include the first evidence among pre-Permian conifers for dorsiventral, bilaterally symmetrical, axillary, fertile shoots, and true inverted ovules with bilateral symmetry (Mapes and Rothwell, 1984).

The original description of *E. lockardii* not only provided the basis for understanding the reproductive biology of primitive conifers but also questioned the validity of some of the characters used to identify species (Mapes and Rothwell, 1984). The Mapes and Rothwell (1984) study in combination with those of Schweitzer (1963, 1996), Clement-Westerhof (1984, 1987), Cuneo (1985), Archangelsky and Cuneo (1987), Kerp et al. (1990), Meyen (1997), Hernandez-Castillo et al. (2001b), and Rothwell and

Mapes (2001) have set the standard for describing and understanding species delimitation among primitive walchian conifers. Additional studies of conifers from Europe (Clement-Westerhof, 1987; Visscher et al., 1986; Kerp and Clement-Westerhof, 1991; Broutin and Kerp, 1994; Kerp et al., 1996), North America (Mapes and Rothwell, 1991; Hernandez-Castillo et al., 2003) also questioned the validity of several of Florin's assumptions.

As a result of the different interpretations drawn from these studies, new and far more rigorous methods for recognizing and characterizing species based on the reconstruction of complete plants were proposed (Hernandez-Castillo et al., 2001b). The new families Bartheliaceae (Rothwell and Mapes, 2001), Thucydiaceae (Hernandez-Castillo et al., 2001b), were added to the previously described families of walchian conifers (i.e., Walchiaceae, Clement-Westerhof, 1984; Emporiaceae, Mapes and Rothwell, 1991, 2003; Utrechtiaceae, Mapes and Rothwell, 1991, Rothwell and Mapes, 2003). The description of the Bartheliaceae and Thucydiaceae showed that completely reconstructed conifers have combinations of characters that defy conventional species, genera, and even familial circumscriptions (Rothwell and Mapes, 2001; Hernandez-Castillo et al., 2001a, 2001b). The new whole plant reconstruction of *E. lockardii* again shows broad ranges of morphological and cuticular variation within a single fossil conifer taxon (Table 1) and a different combination of characters for walchian conifer species (Tables 3-5). The reconstruction also demonstrates that our previous knowledge based on morphotaxa is biased because isolated organs do not reflect the suite of characters present in a single whole plant reconstruction.

Thus, morphotaxa of walchian conifers are useful to describe isolated and/or fragmentary conifer organs at a given locality, but they cannot be used as whole plants or to propose phylogenetic inferences (e.g., Clement-Westerhof, 1988). This study also confirms that some concepts of "natural taxa" (sensu Visscher et al., 1986) such as *Walchiostrobus* Florin and *Culmitzchia* Ullrich are not equivalent to complete plants. The use of whole plants based on accurate reconstructions is essential for understanding the systematics of Upper Carboniferous and Permian primitive conifers worldwide.

Systematic Relationships - The reconstruction of *E. lockardii* presented here includes the following combination of characters: 1) plagiotropic lateral branches, 2) simple and forked leaves on penultimate branches (= age dependent heterophylly), 3) simple leaves on ultimate shoots with two adaxial bands of stomata and abaxial short or narrow stomatal bands or single rows of stomata, 4) endarch stele, 5) resin rodlets in ground tissues, 6) uniseriate-biseriate circular bordered pits on secondary xylem tracheids, 7) uniseriate to biseriate wood rays, 1-8 cells high, 8) simple, terminal pollen cones, 9) peltate microsporophylls with adaxial pollen sacs, 10) monosaccate, *Potonieisporites* Bharadwaj type of prepollen grains, 11) compound, terminal ovulate cones, 12) forked bracts in ovulate cones, 13) axillary, ovuliferous, dwarf shoots free from bract, 14) dwarf shoots dorsiventral and bilaterally symmetrical, 15) dwarf shoots with 14-30 sterile scales, and 1-3 sporophylls, 16) ovules bilateral, winged, and 17) simple pollen chamber with nucellar beak.

While the character combination in *E. lockardii* is unique among completely reconstructed walchian conifers, many of these characters also occur in other walchian species (Table 1). Since traditionally walchian conifers have been described as morphotaxa based on isolated organs such as branches, pollen cones or ovulate cones that are usually fragmentary (Florin, 1938-45; Broutin and Kerp, 1994), many of the comparisons in the literature are done organ by organ without reaching a whole plant comparison (Clement-Westerhof, 1984, 1987; Mapes and Rothwell, 1984; Winston, 1984; Kerp and Clement-Westerhof, 1991; Broutin and Kerp, 1994; Kerp et al., 1996; Meyen, 1997; Lausberg and Kerp, 2000). In this study, both vegetative and fertile organs of *Emporia lockardii* show the ranges of variation of leaves and leaf-like structures within a single conifer plant (Table 1). *Emporia lockardii* is compared to some of the most well known taxa of the Walchian, Angaran, and Voltzian Voltziales clades (Tables 1-4; Rothwell et al., 2005). These comparisons are summarized at the whole plant level (Table 2) and at the individual organ level using vegetative (Table 3), cuticular (Table 4), and ovulate cone/zone (Table 5) characters.

Ranges of variation among the different organs of *Emporia lockardii* show that leaves of all orders are simple with the exception of those on penultimate shoots, and bracts on ovulate cones (Table 1). All leaves on penultimate and ultimate shoots are basically narrowly triangular to linear in face view, and slightly concave to slightly S-shaped in side view regardless of their location, with the exception that sterile scales range from elliptical to widely ovate in shape in face view (Table 1). Sizes of leaves indicate that bracts on ovulate cones are the largest followed by smaller leaves on penultimate shoots, and leaves on ultimate shoots, microsporophylls and then sterile scales in that order (Table 1). Size of leaves on penultimate shoots is comparable to attached leaves on shoots bearing ovulate cones, while leaves on ultimate shoots (including those bearing pollen cones) are comparable to sterile scales (Table 1). All leaves are amphistomatic with two long bands of adaxial stomata and two short, narrow bands of abaxial stomata or individual rows of stomata (Table 1). Similarly, leaves may have 2-5 stomata per stomatal band with the exception of leaves on ultimate shoots (up to 8), and microsporophylls (2-4) on pollen cones (Table 1). However, the number of subsidiary cells per stomatal complex differs among leaves, ranging from 4-5 in microsporophylls to 5-9 in leaves borne on ultimate shoots (Table1). The distribution of papillae and trichome bases are basically the same for most organs (Table 1), indicating that isolated organs of *Emporia lockardii* may be recognized by their leaf morphology and cuticular features at the Hamilton Quarry. However, this is only possible now that the overall variation within this plant is known. Nevertheless, caution must be taken when more than one plant is found at the same locality, and ranges of variation within other possible taxa must be assessed.

Emporia lockardii shares characters with other walchian conifers such as lateral plagiotropic branches with simple (*Ernestiodendron filiciforme* (Florin) Florin, *T. mahoningensis*) or forked leaves (*Hanskerpia hamiltonensis* Rothwell et Mapes, *Utrechtia floriniformis* (Mapes et Rothwell) Rothwell et Mapes, and *O. hypnoides*) on penultimate shoots (Table 2), and simple leaves on ultimate shoots (all except for *Barthelia furcata* Rothwell et Mapes that has simple and forked leaves) (Table 2). Additional characters shared by *E. lockardii* are terminal ovulate cones (*H. hamiltonensis*, *U. floriniformis*, *O. hypnoides*, *E. filiciforme*), and simple pollen cones in all taxa with the exception of *T. mahoningensis* that has compound pollen cones (Hernandez-Castillo et al., 2001a, 2001b).

Emporia lockardii is most similar to the European walchian conifers *U. floriniformis* and *O. hypnoides* (Table 1). *Utrechtia floriniformis* differs from *E. lockardii* by having forked leaves on penultimate shoots, position dependent heterophylly, two bands of abaxial stomata on ultimate shoot leaves, and terminal sporophylls (Table 1). These characters contrast with simple to forked leaves on penultimate shoots, age and position dependent heterophylly, varying abaxial stomatal distribution, and the number of sporophylls interspersed with sterile scales in *E. lockardii* (Table 1). *Otovicia hypnoides* differs from *E. lockardii* by having forked leaves on penultimate shoots, position dependent heterophylly, and primarily adaxial stomata with scattered abaxial stomata (Table 1).

Rothwell and collaborators (2005) reconstructed and described *Hanskerpia hamiltonensis* from the Hamilton Quarry, and undertook the first phylogenetic analysis of these primitive conifers using the most well known voltzialean conifers. According to this phylogenetic analysis, the order Voltiziales can be divided into the following clades: Walchian (Upper Carboniferous-Lower Permian), Gondwanan (Lower Permian), Angaran (Middle-Upper Permian), and Voltzian (Late Permian and Triassic) Voltziales (Fig. 10 of Rothwell, 2005). These clades support some previous hypotheses of relationships among primitive conifers but are not consistent with others (Rothwell et al., 2005). For example, the "Walchian Voltziales"(Rothwell et al., 2005) are a paraphyletic assemblage that includes the Lebachioid clade and *E. filiciforme* and *T. mahoningensis*. The Lebachioid clade is well resolved but is comprised of typical European (*E. filiciforme*, *O. hypnoides* and *U. floriniformis*), and North American walchians (*Emporia* spp., *H. hamiltonensis*, and *T. mahonigensis*), and coniferophytes (*B. furcta*) that are placed in three different families (Utrechtiaceae Rothwell et Mapes, 2003 or Walchiaceae sensu Clement-Westerhof 1984; Emporiaceae Mapes et Rothwell, 2003; Bartheliaceae, Rothwell et Mapes, 2001). Indicating that current familial circumscriptions among these walchian Voltiziales are not supported by the analysis (Rothwell et al., 2005).

Emporia lockardii is most similar to *O. hypnoides* and *U. floriniformis* in this study and supports the phylogeny proposed by Rothwell et al. (2005), where *O. hypnoides* and *U. floriniformis* are sister to *E. lockardii.* Differences between the Utrechtiaceae and Emporiaceae are based on two characters, the number and position of sporophylls on axillary dwarf shoots (Table 2). Thus, are the Emporiacae and the Utrechtiaceae (= Walchiaceae) distinct families of walchian conifers?

Systematic Relationships of the Utrechtiaceae and Emporiaceae. It is clear that both the Utrechtiaceae (= Walchiaceae) and Emporiaceae have very similar diagnostic characters (Table 2; Clement-Westerhof, 1984; Kerp and Clement-Westerhof, 1991; Mapes and Rothwell, 1991; Mapes and Rothwell, 2003; Rothwell and Mapes, 2003). An extensive discussion on the history, nomenclature, and additional rationale for the emendation and description of both families can be found in Clement and Westerhof (1984), Mapes and Rothwell (1991), Hernandez-Castillo et al. (2001b), and Rothwell et al. (2005). Therefore, our goal here is not to repeat that information but to analyze the diagnostic characters of both families in light of the newly described walchian conifer species (e. g., *T. mahoningensis*) and the new material from the Hamilton Quarry.

The mode of preservation of the fossils has played an important role in distinguishing these families through the years. While the Utrechtiaceae (= Walchiaceae) is based on impression/compressions with cuticular remains, the Emporicaceae is based on impression/compressions with cuticles and permineralized specimens that allow for anatomical details of stems and cones (Mapes and Rothwell, 1984). These anatomical features of the Emporiaceae led previous authors to be cautious in placing *Emporia lockardii* in the Utrechtiaceae (= Walchiaceae) or suggesting that members of the Utrechtiaceae (= Walchiaceae) actually belonged to the Emporiaceae (i.e., *Ernestiodendron*, *Otovicia*) (Kerp et al., 1990; Mapes and Rothwell, 1991).

Originally, the Emporiaceae was distinguished from the Utrechtiaceae (= Walchiaceae sensu Clement-Westerhof, 1984) in having more than one ovule (1-3) and sporophylls or fertile scales interspersed with sterile scales per axillary dwarf shoot (Clement-Westerhof, 1984; Mapes and Rothwell, 1991). Later, after considering the description of *O. hypnoides*, Kerp and collaborators (1990) realized that it was possible to have two ovules on the axillary dwarf shoot, modifying the number of sporophylls present in the family, and reducing the number of diagnostic characters that separate these families (Table 2).

In this dissertation, the Emporiaceae has one to three sporophylls interspersed with sterile scales (chapters 4 and 5 in this dissertation), while the Utrechtiaceae (= Walchiaceae) has one terminal sporophyll (*U. floriniformis*) or two interspersed sporophylls (*O. hypnoides*) (Tables 1, 4). This indicates that the number and position of sporophylls overlaps with that of the best known taxa (*O. hypnoides* and *U. floriniformis*) within the Utrechtiaceae (= Walchiaceae), leading basically to the same suite of characters for both families (Tables 1, 4). If the difference between these two families is based only in two overlapping characters it may indicate that they are indeed a single family of ancient conifers. However, before proposing taxonomic changes to the already conflicting classifications, additional conifers from both families need to be reconstructed. Moreover, a complete analysis of the ranges of variation among different characters has to be performed to understand and delimit these walchian conifers. Future research should focus on a better understanding of the following characters: 1) lateral branch shape and size, 2) leaf morphology on different orders of branches, 3) cuticular features of all leaves and leaf-like organs within a single plant, 4) pollen sac position and variation among prepollen grains (i.e., size, shape), 4) ovulate cone architecture and position, and 5) axillary dwarf shoot organization and sporophyll number and position.

Age dependent heterophylly - Walchian conifers are represented by plants with plagiotropic lateral branches composed of a penultimate shoot that bears several ultimate shoots with helically arranged leaves. Emphasis has been placed on the presence of simple or forked leaves on penultimate shoots that contrast with simple leaves on ultimate shoots. This difference between the shape of the leaves (forked vs. simple) on penultimate and ultimate shoots of walchian conifers has been reported as heterophylly (Hernandez-Castillo et al., 2001b; Rothwell et al. 2005). This definition differs from that of other authors who refer to heterophylly as a difference in leaf size (e.g., Kerp et al. 1990). Thus, heterophylly may be dependent on the position of the leaves (e.g., leaves on penultimate shoots, *U. floriniformis*) or size of the leaves (e.g., leaves on penultimate and ultimate shoots, *B. furcata*) (Table 2). *Emporia lockardii* has simple leaves on all ultimate shoots (1.7-5.0 mm long), simple leaves on vegetative penultimate shoots (5-7 mm long), and forked leaves on fertile penultimate shoots (8-10 mm long). The diameter of vegetative penultimate shoots ranges from 1.2-3.5 mm, while that of penultimate shoots below the ovulate cones ranges from 3.4-4.0 mm. Indicating that leaves on penultimate shoots and ultimate shoots are different (position-dependent heterophylly) and that forked leaves are only borne on large penultimate axes like those that bear ovulate cones (size-dependent heterophylly). Therefore, there is a position dependent heterophylly in *E. lockardii* but this heterophylly also depends on the size of the stem.

Forked leaves on penultimate shoots of *E. lockardii* are found only on large lateral branches. Large lateral branches, similar to those of *E. lockardii,* are frequently found at the base of juvenile trees of *Araucaria heterophylla* (Salisb.) Franco and recently reconstructed walchian conifers (Hernandez-Castillo et al., 2003, chapter 2 in this dissertation; Lausberg, 2002). Then forked leaves of *E. lockardii* are most probably located on basal or old branches suggesting an age-dependent heterophylly. Although trees of *E. lockardii* and other walchian conifers were probably trees of small stature (Hernandez-Castillo et al., 2003; Lausberg, 2002), they seem to be switching from size- or position-dependent heterophylly to age-dependent heterophylly. Age-dependent heterophylly has not been reported in walchian conifers before but is well known in living species conifers particularly in the Araucariaceae, Cupressaceae s. l., and some Podocarpaceae (Chamberlain, 1935; de Laubenfels 1972; Veillon, 1978; Falder, 1999; Grosfeld et al., 1999; Hernandez-Castillo, 2003).

A reexamination of walchian conifers with simple and forked leaves on penultimate shoots is needed to confirm if other walchian conifers have age dependent heterophylly. To date, most conifers have been described as having either simple (i.e., *E. filiciforme*, *T. mahoningensis*, *L. garnettensis*) or forked (i.e., *U. floriniformis*, *O. hypnoides*, *B. furcata*, *H. hamiltonensis*) leaves on penultimate shoots (Florin 1938-45, 1951; Kerp et al., 1990; Schweitzer, 1996; Mapes and Rothwell, 1991; Hernandez-Castillo et al., 2001b; Mapes and Rothwell, 1991, 2003; Rothwell and Mapes, 2001, 2003; Rothwell et al., 2005), but no correlation has been found between the diameter of penultimate stems and the presence of simple or forked leaves in any of these species. Age dependent heterophylly may not be unique to *E. lockardii* but more research has to be done on the previously described species to confirm or refute its presence in other Paleozoic conifers.

Conclusions. *Emporia lockardii* is a small orthotropic plant bearing lateral branches that bear helically arranged, simple to forked leaves on penultimate shoots and simple leaves on ultimate shoots. This is the only walchian conifer with age-dependent heterophylly and one of the few where morphological and cuticular ranges of variation are known for all leaf-like structures within the plant. This plant has terminal, simple pollen cones with adaxial pollen sacs, *Potonieisporites* Bharadwaj (1964) type of prepollen grains, and terminal, compound ovulate cones with forked bracts, and bilaterally symmetrical axillary dwarf shoots with one to three sporophylls and a single ovule/seed per sporophyll. Diagnostic characters of the Emporiaceae closely resemble those of the Utrechtiaceae (= Walchiaceae sensu Clement-Westerhof) and they may represent a single family of Euramerican "walchian Voltziales". However, no taxonomic changes can be addressed before additional taxa from both families are reconstructed. *Emporia lockardii* is the third conifer reconstructed from the Hamilton Quarry and together with two more taxa from the same family that are being described elsewhere (chapters 4 and 5 in this dissertation), make the Emporiaceae the best known family of walchian conifers from Euramerica. The Hamilton Quarry is the only locality in the world were most conifer species are described as whole plants.

Table 1. Comparison of morphological and cuticular characters of leaves on vegetative and fertile organs of *Emporia lockardii*.

Organs/ Characters	Shape (face view)	Shape (side view)	Length (mm)	Width (mm)	Stomata				Papillae		Trichome bases (adx / abx)
					Structure	Distribution (adaxial / abaxial)	Number of stomata per band	Subsidiary cell number	Subsidiary cells	Epidermal cells	
Leaves on antepenultimate shoots	?	?	?	?	?	?	?	?	?	?	?
Leaves on penultimate shoots	Nt, Li, Fr	Sc, Sss	5 - 10	1.0 - 2.1	Monocyclic	Two long bands / two short, narrow bands or ind. rows	2 - 5	6 - 8	Erect,	Few or none	Few, none / abundant
Leaves on ultimate shoots	Nt, Li	Sc, Sss	1.7 - 5.0	0.4 - 1.1	Monocyclic	Two long bands / two narrow bands or ind. rows	2 - 5 (8)	5 - 9	Overarching	Few to abundant	Few, none / abundant
Leaves on branches with attached to pollen cones	Nt, Sl, Li	Sc, Sss	3 - 5	1.6 - 2.2	Monocyclic	Two long bands / two ind. rows	2 - 5	5 - 7	Overarching	Few or none	Few, none / abundant
Microsporophylls	Tr	Sc	0.25 - 5.0	2 - 3	Monocyclic	Two long bands / few scattered or none	2 - 4	4 - 5	Overarching	Abundant	None / abundant
Leaves on branches with attached to ovulate cones	Nt, Li, Fr	Sc, Sss	7 - 10	1 - 2.1	Monocyclic	Two long bands / two short, narrow bands or ind. rows	2 - 5	6 - 8	Erect	Few or none	Few, none / abundant
Bracts of ovulate cones	Nt, Li, Fr	Sc, Sss	8 - 21	2 - 3	Monocyclic	Two long bands / two short, narrow bands or ind. rows	2 - 5	6 - 8	Erect	Few or none	Few, none / abundant
Sterile scales of ovulate cones	El, l, Wo	Sc, Sss	2.1 - 4.3	1.3 - 1.8	Monocyclic	Two long bands / two narrow bands or ind. rows	2 - 5	6 - 7	Erect, overarching	Few or none	Few, none / abundant

Leaf shape abbreviations: El = Elliptical, Fr = Forked Tip, Li = Linear, l = Lanceolate, Ns= Narrow sub-triangular, Nt = Narrowly triangular, Ob= Oblong, Ov= Ovate, Wo = Widely oblong, Sc = Slightly concave, Sl= Slightly lanceolate, Sp= Spreading (extending nearly to the horizontal), Sq= Squamose (=scale like), Ss = S-shaped, Sss = Slightly S-shaped, St= Sub-triangular, Tr= Triangular.

Table 2. Comparison of morphological and cuticular characters of *Emporia lockardii* and other Paleozoic conifers and coniferophytes. Characters that differ from those of *E. lockardii* are recorded in bold face type.

Species/ Characters	**Lateral branches**	**Penultimate leaves**	**Ultimate leaves**	***Hetero-phylly**	**Stomatal distribution (vegetative leaves)**	**Stomatal pattern Adx / Abx**	**Compound ovulate organ**	**Bract and ovuliferous dwarf shoot**	**Sporophyll position / number**	**Pollen Cone**	**Microsporophylls**	**Pollen Sacs**
Emporia lockardii	Plagiotropic	Simple and forked	Simple	Age and position dependent	Amphistomatic	Two bands / two short, narrow, ind. rows	Cone	Separate throughout	Interspersed with SS, 1-3	Simple	Simple	Adaxial
Hanskerpia hamiltonensis	Plagiotropic	**Forked**	Simple	**Position dependent**	Amphistomatic	**Parallel rows / parallel rows**	**Cone/zone?**	**Fused at base**	Interspersed with SS, 1-2	?	?	?
Thucydia mahoningensis	Plagiotropic	**Simple**	Simple	**Absent**	**Adaxial**	Two bands / **absent**	**Fertile zone**	Separate throughout	**Terminal, 3-4**	**Compound**	Simple	**Terminal**
Utrechtia floriniformis	Plagiotropic	**Forked**	Simple	**Position dependent**	Amphistomatic	Two bands / **two bands**	Cone	Separate throughout	**Terminal, 1**	Simple	Simple	Adaxial
Otovicia hypnoides	Plagiotropic	**Forked**	Simple	**Position dependent**	**Primarily adaxial**	Two bands / **scattered**	Cone	Separate throughout	Interspersed with SS, 2	Simple	Simple	Adaxial
Ernestiodendron filiciforme	Plagiotropic	**Simple**	Simple	**Absent**	Amphistomatic	**Parallel rows / parallel rows**	Cone	Separate throughout	**Terminal, 1**	Simple	Simple	?
Barthelia furcata	**Irregular**	**Forked**	**Simple and forked**	**Size dependent**	**Adaxial**	Two bands / **absent**	**Fertile zone**	Separate throughout	Interspersed with SS, ?	Simple	**Forked**	Adaxial

Modified from Rothwell et al., 2005. * Heterophylly is based on differences in the shape of leaves, where two distinctive types of leaves are known. Adx = adaxial surface, Abx =abaxial surface, SS = sterile scales.

Table 3.Comparison of leaves using morphological characters of *Emporia lockardii*. Characters that differ from those of *E. lockardii* are recorded in bold face and overlapping characters are recorded in italics.

Species/ Characters	Stem	Lateral branches	Penultimate leaves				Ultimate leaves						*Heterophylly
			Length (mm)	Width (mm)	Shape (face view)	Shape (side view)	Length (mm)	Width (mm)	Shape (face view)	Shape, (side view)	Angle of Divergence Base	Apex	
[1] *Emporia lockardii*	Orthotropic?	Plagiotropic	5-10	1.0-2.1	Nt, Li, Fr	Sc, Sss	1.7 - 5.0	0.4-1.1	Nt, Li	Sc, Sss	26-63	28-69	Present
[2] *Hanskerpia hamiltonensis*	Orthotropic?	Plagiotropic	**13-29**	*1.0-1.74*	*Li, Fr*	**Sp**	**5-15**	*0.6-1.1*	*Li*	*Sc*, **Sp**	*30-45*	**32-50**	Present
[3] *Thucydia mahoningensis*	Orthotropic	Plagiotropic	*5.0-12.5*	*1.0-1.5*	*Nt, Li*	*Sc, Ss*	*3.0-6.0*	*0.4-1.0*	Nt, Li	[a] *Sc*, **Ss**	*22-57*	**21-54**	**Absent**
[4] *Utrechtia floriniformis*	Orthotropic?	Plagiotropic	**12.0-25.0**	*1.5-3.0*	Nt, Li, Fr	*Sc*	*9.0-13.0*	*0.4-0.6*	Nt, Li	*Sc*, **Ss**	?	**30**	Present
[5*] *Lebachia garnettensis*	?	Plagiotropic	*3.0-16.0*	*1.5-2.5*	*Nt, Li*	*Sc*	*4.0-7.0*	*0.4-1.4*	Nt, Li	*Sc*, **Ss**	*35-70*	?	**Absent**
[6] *Otovicia hypnoides*	?	Plagiotropic	*2.0-8.0*	*1.0-1.5*	**St, La**, *Fr*	[a] **Fa, Ss**	*1.5-4.0*	*0.2-0.5*	Nt, Li	[a] **Fa**	*35-90*	**35**	Present
[2] *Ernestiodendron filiciforme*	?	Plagiotropic	**10.0-23.0**	*1.5-3.5*	*Nt, Li*	[b]*Sc*, **Sp**	**7-15**	*1.5-2.0*	Nt, Li	**Sp**	**70-110**	**15**	**Absent**
[7] *Barthelia furcata*	?	**Irregular**	**22-47**	**<4.0**	*Li, Fr*	**Li**, *Sc*	**10-25**	**Up to 4.0**	*Li*	**Li**, *Sc*	*25-35*	**14-25**	Present
[8] *Kungurodendron sharovii*	?	**Plagiotropic to Irregular?**	*?-12.0*	*?-3.5*	**Tr, La**	*Sc*	**4-9**	*1.0-1.25*	**Tr, La**	**Li**, *Sc*	*>30*	?	**Absent**
[8] *Concholepis harrisii*	?	**Irregular**	*?-12.0*	*?-2.5*	**Tr ?**	[a] **Fa**, *Sss*	?	?	**Tr ?**	[a] **Fa**, *Sss*	*40-45*	?	**Absent?**
[8] *Timanostrobus muravievii*	?	**Irregular**	?	?	**La, Sq**	*Sc*	?	?	**La, Sq**	*Sc*	*>30*	?	**Absent?**
[9] *Voltzia hexagona*	?	**Irregular**	**60- 150**	**15-50**	*Li*, **Tr**	*Sc*	*45-60	**15-30**	*Li*, **Tr**	*Sc*	*20-45*	?	Present
[10] *Majonica alpina*	?	?	**?-35.0**	**?-6.0**	**Ns, Ov**	?	**10-30**	**3-4**	**Ov**	**Sl**	?	?	**May occur?**
[10] *Dolmitia cittertiae*	?	?	?	?	?	?	**8-20**	**4-5**	**Ov, Ob**	?	?	?	?
[11] *Ortiseia leonardii*	?	*Plagiotropic*	**12.0-35.0**	**?-8.0**	**Ob, Ov**	**Sl**	**6-15**	**4-7**	**El, Ov**	**Sl**	*20-45*	?	**Absent**

Modified from Hernandez-Castillo et al., 2001b. [1] Including measurements of Mapes and Rothwell, 1984, 1991. [2] Florin 1938-45. [3] Hernandez-Castillo et al 2001 b. [4] Mapes and Rothwell 1991. [5*] Emended by Winston (1984). [6] Kerp et al. 1990; however, leaf measurements were taken from Florin (1938-45) because such data are not available in Kerp et al. 1990. [7] Rothwell and Mapes 2001. [8] Meyen, 1997, angles estimated from plates. [9] Schweitzer, 1996; however, measurements of leaves were taken directly from the plates. [10] Clement-Westerhof, 1987. [11] Clement-Westerhof, 1984.

Leaf shape abbreviations: El = Elliptical, Fr = Forked Tip, Li = Linear, Ns= Narrow sub-triangular, Nt = Narrowly triangular, Ob= Oblong, Ov= Ovate, Sc = Slightly concave, Sl= Slightly lanceolate, Sp= Spreading (extending nearly to the horizontal), Sq= Squamose (=scale like), Ss = S-shaped, Sss = Slightly S-shaped, St= Sub-triangular, Tr= Triangular.
[*] Heterophylly is based on differences in the shape of leaves, where two distinctive types of leaves are known. However, Kerp et al. 1990 may use the same term to emphasize differences in leaf size.

[a] Slightly concave (Sc) and S-shaped (Ss) are leaf shapes in the sense of Florin's monograph. According to Florin's monograph (1938-45), leaves of *Lebachia* are 1) slightly concave, where the adaxial side is slightly curved and concave and the tip is incurved at different angles; 2) "S-shaped" where the half of the adaxial side is first concave and then bent forward-inwards with a pointed tip; and 3) a combination of both general types. [b] *Ernestiodendron filiciforme* (Florin, 1938-45) has spreading leaves, where leaves are rotate, more or less firm, where the apical portion of the adaxial side is slightly bent and concave, or slightly convex, and the tip is parallel to the main axis of the stem and or slightly concave to it, or incurved at an angle of 15 degrees. [c] According to Kerp et al (1990) and Meyen (1997) leaves may be falcate (Fa), however the definition for falcate refers to a slightly convex sickle shape, in which the tip of the object (e.g. leaf) is recurved away from the stem and not incurved toward the stem. Therefore, falcate in the sense of those authors is incorrectly applied, and is equal to slightly concave in the sense of Florin.

Table 4. Comparison of cuticular features of leaves on ultimate shoots of *Emporia lockardii* and other Paleozoic conifers. Characters that differ from those of *E. lockardii* are recorded in bold face type.

Species/ Characters	General Group	Stomatal distribution adaxial	Stomatal distribution abaxial	Stomatal complex structure	Stomatal complex size (µm)	Subsidiary cell number	Subsidiary cell papillae	Marginal trichomes	Trichome bases adaxial	Trichome bases abaxial	Epidermal papillae adaxial	Epidermal papillae abaxial
[1] *Emporia lockardii*	*Walchian Voltziales*	Two long bands	Two short, narrow, ind. rows	Monocyclic	58 x 46	5 - 9	Present	Present, short and long	Few or absent	Present abundant	Present	Present
[2] *Hanskerpia hamiltonensis*		**Parallel rows**	**Parallel rows**	Monocyclic	**30 x 70**	*5 - 6*	Present	**Present, short**	*Present*	Present abundant	Present	Present
[3] *Thucydia mahoningensis*		Two long bands	**Absent**	Monocyclic	**24 x 20**	*6 - 8*	Present	*Present, short, long,* **hair-like**	Absent	Present, abundant	Present	**Absent**
[4] *Utrechtia floriniformis*		Two long bands	**Two short bands, variable**	Monocyclic	**50 x 55**	5 - 9	Present	*Present, short,* **hair-like**	*Present*	Present, abundant	Present	Present
[5] *Lebachia garnettensis*		Two long bands	**Few, scattered**	Monocyclic	*45 x 40	**More than 10?**	**Absent**	*Present, short,* **hair-like**	Absent	Present abundant	?	?
[6] *Otovicia hypnoides*		Two long bands	**Few stomata groups**	*Monocyclic,* **incompletely dicyclic**	**70 x 60**	*5 - 8*	Present	**Present, conical**	*Present*	Present abundant	Present	Present
[2] *Ernestiodendron filiciforme*		**Parallel rows**	**Parallel rows**	*Monocyclic,* **incompletely dicyclic**	*60 x 40	*4 - 8*	Present	*Present, short,* **hair-like**	*Present*	Present abundant	**Absent**	Present
[7] *Barthelia furcata*		Two long bands	**Absent**	Monocyclic	**36 x 63**	*4 - 7*	Present	*Present, short,* **hair-like**	*Present*	Present, abundant	Present	Present
[8] *Kungurodendron sharovii*	*Angaran Voltziales*	Two bands	**Few stomata groups**	Monocyclic	?	*5 - 8*	**More or less**	*Present, short,* **papilla-like**	*Present*	**Absent**	Present	**Absent**
[8] *Concholepis harrisii*		?	?	?	?	?	?	**Present?**	?	?	?	?
[8] *Timanostrobus muravievii*		**Indistinct short rows, scattered**	**Indistinct short rows, scattered**	Monocyclic	?	*5 - 6*	**Absent?**	*Present, short*	?	?	?	?

[9] *Voltzia hexagona*		?	?	?	?	?	?	?	?	?	?	?
[10] *Majonica alpina*	*Late Permian Voltziales*	**Interrupted rows**	**Interrupted rows to no rows**	?	**75**	*5 - 10*	Present	**Absent**	?	?	Present?	Present?
[10] *Dolmitia cittertiae*		**Interrupted rows or scattered**	**Scattered**	Monocyclic	**90**	*5 - 10*	Present	***Present, short* and wide**	?	?	?	**Sometimes**
[11] *Ortiseia leonardii*		**Parallel rows**	**Parallel rows**	**Dicyclic**	65	*4 - 7*	Present	**Absent?**	**Present abundant**	Present abundant	Present	Present

Modified from Hernandez-Castillo et al., 2001b.[1] Mapes and Rothwell, 1984, 1991. [2] Florin 1938-45. [3] Hernandez-Castillo et al 2001 b. [4] Mapes and Rothwell 1991. [5*] Emended by Winston (1984). [6] Kerp et al 1990; however, leaf measurements were taken from Florin (1938-45) because such data are not available in Kerp et al 1990. [7] Rothwell and Mapes 2001. [8] Meyen, 1997, angles estimated from plates. [9] Schweitzer, 1996; however, measurements of leaves were taken directly from the plates. [10] Clement-Westerhof, 1987. [11] Clement-Westerhof, 1984.[*] Measured directly from Florin's monograph (1938-45).

Table 5. Characters of compound ovulate cones and zones of *Emporia lockardii* and those of other Paleozoic conifers. Characters that differ from those of *E. lockardii* are recorded in bold face and overlapping characters are recorded in italics.

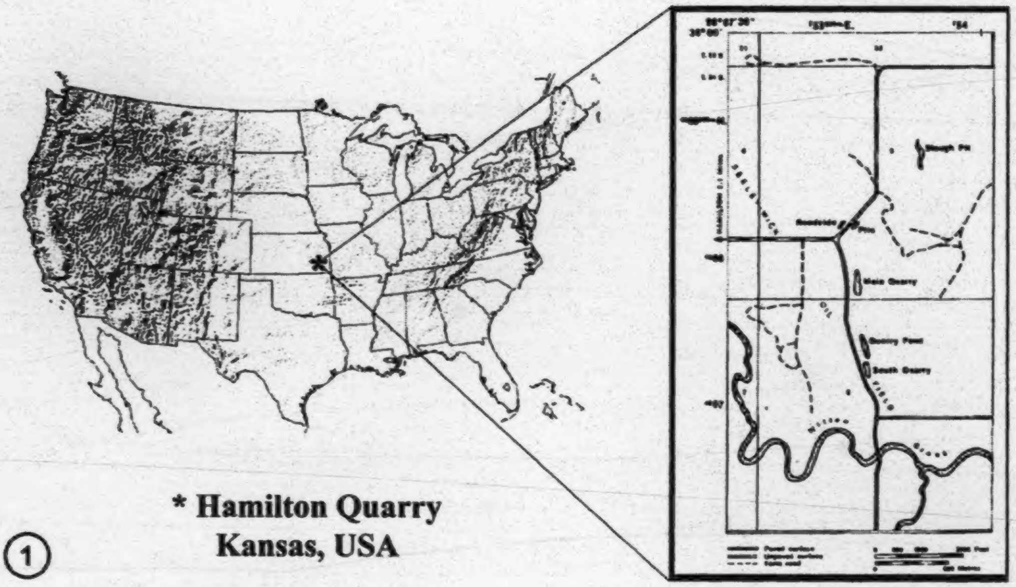
Species/ Characters	General Group	Ovulate Fructification	Cone Morphology			Bract	Dwarf shoot				Ovules
			Length (cm)	Width (cm)	Shape		Symmetry	Number of sterile scales	Position of sporophylls	Number of sporophylls*	
[1] *Emporia lockardii*		Terminal cone	2.8-5.0	1.1-1.5	Cylindrical to ellipsoidal	Forked	Bilateral	14-30	Interspersed with SS	1 - 3	Terminal, Inverted
[2] *Hanskerpia hamiltonensis*	*Walchian Voltziales*	**Terminal cone/zone?**	**11.0**	**2.7**	*Cylindrical*	Forked	Bilateral	*<15?*	Interspersed with SS	*1 - 2*	Terminal, Inverted
[3] *Thucydia mahoningensis*		**Fertile Zone**	*3.0-4.5*	*0.9-1.5*	Cylindrical to ellipsoidal	**Simple**	Bilateral	*10-15*	**Terminal**	3 - 4	Terminal, Inverted
[4] *Utrechtia floriniformis*		Terminal cone	**7.0**	**1.2**	Cylindrical to ellipsoidal	Forked	Bilateral	*>10*	**Terminal**	*1*	Terminal, Inverted
[5] *Lebachia garnettensis*		Terminal cone	*2.0-3.0*	**0.10-0.15**	*Ellipsoidal*	Forked	Bilateral	<5?	?	*≥3?	?
[6] *Otovicia hypnoides*		Terminal cone	**3.0-6.5**	*1.1-1.8*	*Cylindrical*	Forked	Bilateral	*>10*	Interspersed with SS	*2*	Terminal, Inverted
[2] *Ernestiodendron filiciforme*		Terminal cone	**10.0-20.0**	**2.2-3.0**	*Ellipsoidal*	Forked	Bilateral	**5-10**	**Terminal?**	*1*	Terminal, Inverted
[7] *Barthelia furcata*		**Fertile zone**	**Up to 16**	**2.4-2.6**	Cylindrical to ellipsoidal	Forked	**Radial**	?	**Terminal**	?	Terminal, Inverted?
[8] *Kungurodendron sharovii*	*Angaran Voltziales*	?	**Up to 7.0**	**3.0**	Cylindrical to ellipsoidal	**Simple**	****Non-radial**	*>10*	Interspersed with SS	**approx. 10**	Terminal, Inverted
[8] *Concholepis harrisii*		**Fertile Zone**	**Up to 12.0**	?	*Cylindrical?*	**Simple**	****Non-radial**	*>10*	Interspersed with SS	*approx. 2*	Terminal, Inverted?

[8] *Timanostrobus muravievii*		**Terminal cone?**	**Up to 11.0**	**4.0**	Cylindrical	?	**Bilateral**	*>10*	**Interspersed with SS**	**>10**	**Terminal, Inverted**
[9] *Voltzia hexagona*	*Late Permian Voltziales*	**Fertile Zone**	**8.5-10.0**	**3.5-5.0**	Cylindrical to ellipsoidal	**Simple**	**Bilateral**	**<5**	**Terminal**	*3*	**Surficial, Inverted**
[10] *Majonica alpina*		?	?	?	?	**Simple**	**Bilateral**	**1-5**	**Terminal?**	*2*	**Surficial, Inverted**
[10] *Dolmitia cittertiae*		?	?	?	?	**Simple**	**Bilateral**	*>10*	**Terminal?**	*3*	**Surficial, Inverted**
[11] *Ortiseia leonardii*		**Terminal cone?**	**6.0**	**2.0**	Cylindrical to ellipsoidal	**Simple**	**Bilateral**	*>10*	**Interspersed with SS**	*1*	**Surficial? Inverted**
[12] *Batenburgia sakmarica*	*Cathaysian Voltziales*	Terminal cone	*2.4*	**3.1**	Cylindrical to ellipsoidal	**2 Lateral Extensions**	?	**8-12**	?	*1 or 2?*	?

Modified from Hernandez-Castillo et al., 2001b. [1] Mapes and Rothwell, 1984, 1991. [2] Florin 1938-45. [3] Hernandez-Castillo et al 2001 b. [4] Mapes and Rothwell 1991. [5]* Emended by Winston (1984). [6] Kerp et al 1990; however, leaf measurements were taken from Florin (1938-45) because such data are not available in Kerp et al 1990. [7] Rothwell and Mapes 2001. [8] Meyen, 1997, angles estimated from plates. [9] Schweitzer, 1996; however, measurements of leaves were taken directly from the plates. [10] Clement-Westerhof, 1987. [11] Clement-Westerhof, 1984. [12] Hilton and Geng 1998. * Fertile scale as in Florin, Clement-Westerhof (1984) and Kerp et al. (1990). ** Where dwarf shoot symmetry is radial, sterile scales and sporophylls are helically arranged, and sporophyll distal region always facing the adaxial side of the shoot. SS= sterile scales.

Figure captions

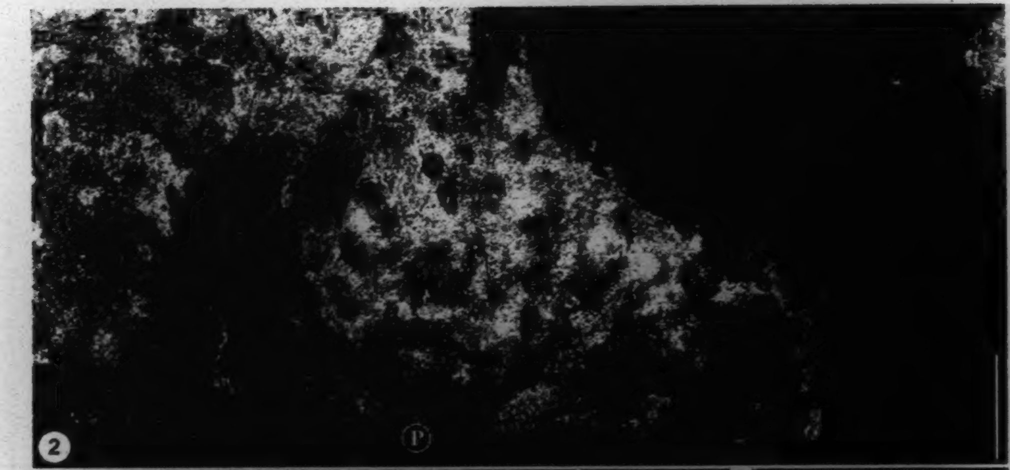
Fig. 1. Map showing location of Hamilton Quarry, Kansas.


Main Quarry
Quarry Pool
South Quarry
Paved surface
Unpaved surface
Earth road

①

* Hamilton Quarry
Kansas, USA

Figs. 2-4. *Emporia lockardii* lateral branches. **2**. Penultimate shoot (p) with several attached ultimate shoots with helically arranged leaves. M 4023, scale bar = 1 cm. **3**. Branch showing general ovoid shape, penultimate shoot (p), and over 36 ultimate shoots with slightly concave to slightly S-shaped leaves. Note portion of apical branch and isolated ovulate cone (upper left). M 1077, scale bar = 2 cm. **4**. Branch showing leaves on penultimate shoots (arrowheads) and several incomplete ultimate shoots with leaves. Note absence of ultimate shoots at base of branch. M 1108A, scale bar = 2.5 cm.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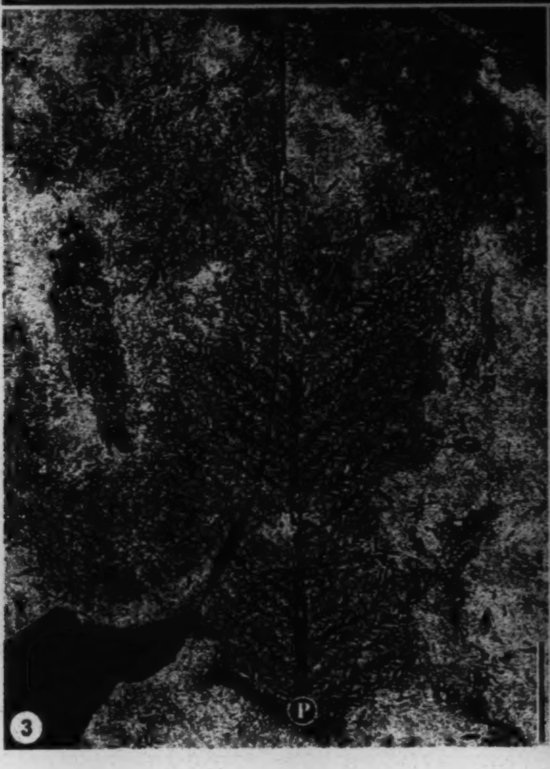
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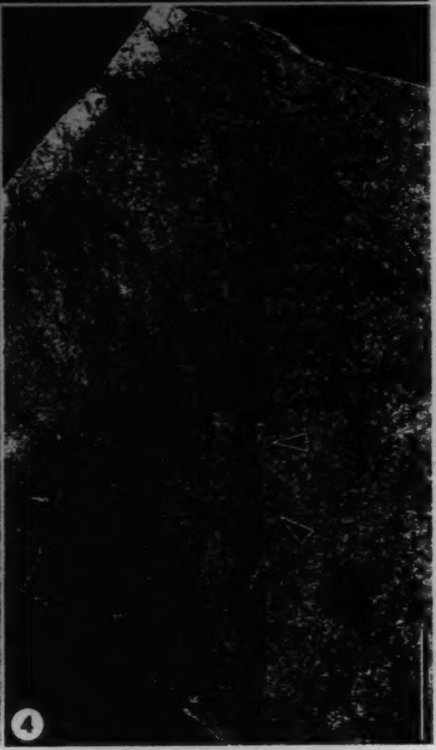
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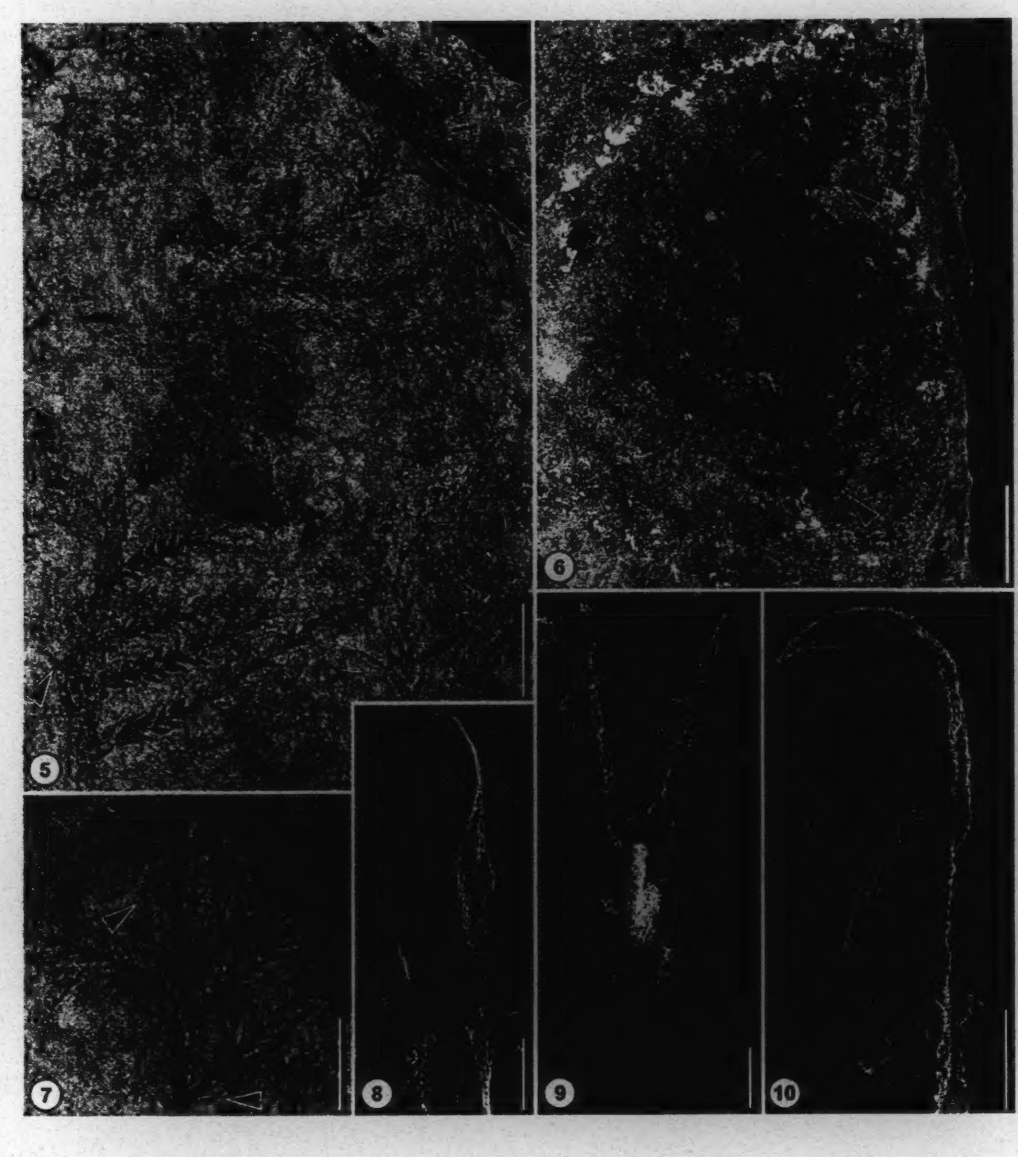
Figs. 5-10. *Emporia lockardii* lateral branches and SEM of leaves. **5**. Leaves on penultimate shoots (arrowhead) and ultimate shoots. M 1028, scale bar = 1 cm. **6**. Branch apex showing deltoid shape and leaves on penultimate shoots (arrowheads). M 2325, scale bar = 1 cm. **7**. Branch showing leaves on penultimate shoots (arrowheads) and ultimate shoots. M 1206A, scale bar = 1 cm. **8**. Penultimate shoot. Leaf showing abaxial surface, linear shape, and slightly curved apex. M1206A scale bar = 1 mm. **9**. Forked leaf from penultimate shoot showing adaxial surface. M 608 A, scale bar = 0.5 mm. **10**. Side view of slightly concave leaf on ultimate shoot with highly incurved apex. M 1206A, scale bar = 0.5 mm.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Figs. 11-14. *Emporia lockardii* cuticular macerations of leaves on penultimate shoots. **11**. Adaxial surface showing narrowly triangular shape. M 897-5, scale bar = 0.5 mm. **12**. Adaxial surface showing two stomatal bands (s), central stomatal free zone. M 897-6, scale bar = 1 mm. **13.** Abaxial surface showing marginal trichomes (arrowhead). M 897-6, scale bar = 0.5 mm. **14.** Adaxial stomatal band showing several stomatal complexes (arrowheads) and numerous epidermal cells separating them (brackets). M 897-1, scale bar = 0.1 mm.

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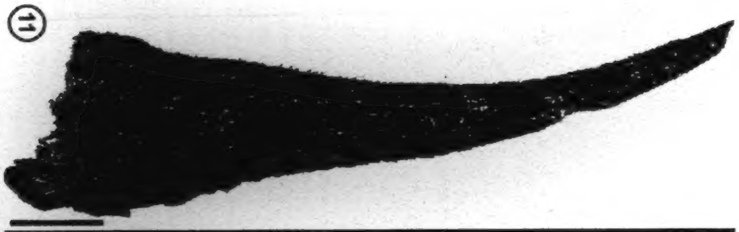

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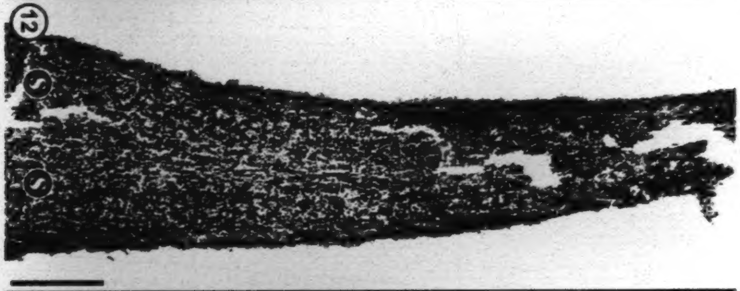

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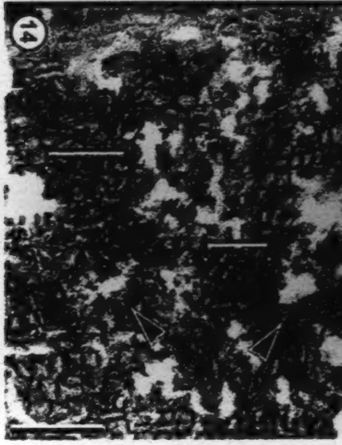

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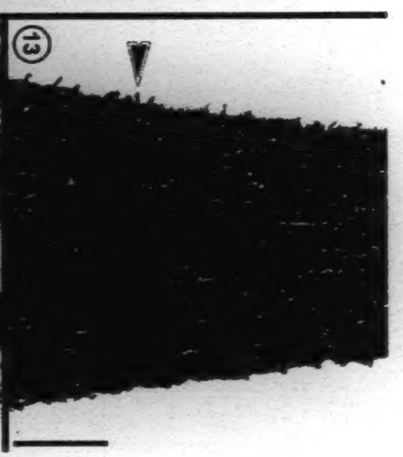
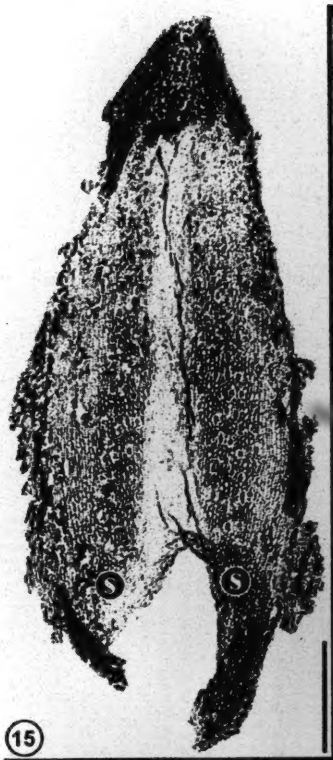


Figs. 15-19. *Emporia lockardii* cuticular macerations of leaves on ultimate shoots. **15**. Adaxial surface showing subtriangular shape, two broad bands of stomata (s) separated by stomatal free zone. M 1188-1, scale bar = 1 mm. **16**. Adaxial surface showing (left to right) elongated epidermal cells with small papillae, stomatal band (s), and elongated epidermal cells of central stomatal free zone. M 2325, scale bar = 0.5 mm. **17**. Adaxial stomatal complexes (s) showing seven to eight subsidiary cells with erect to overarching papillae. M 1188-1, scale bar = 0.1 mm. **18**. Abaxial surface showing numerous trichome bases and narrow marginal stomatal row (s). M 1188-6, scale bar = 0.7 mm. **19**. Abaxial surface showing trichome bases with elongated epidermal cells, and stomata with eight to nine subsidiary cells and overarching papillae. M 1188-6, scale bar = 0.1 mm.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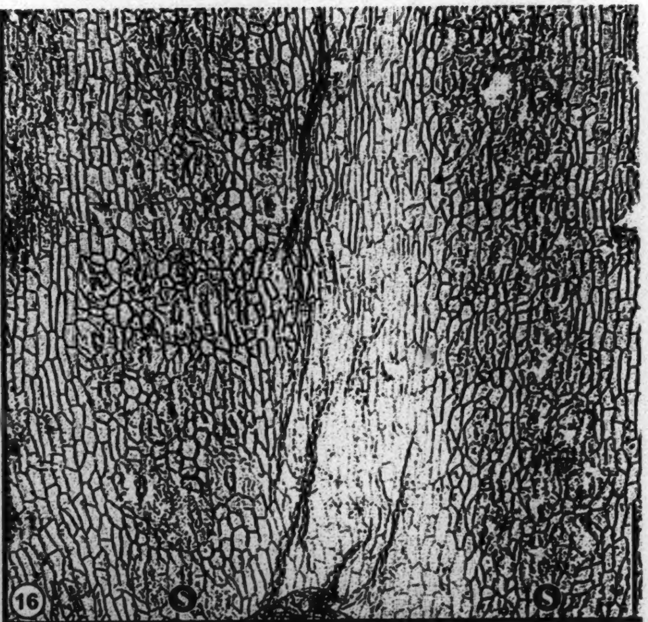
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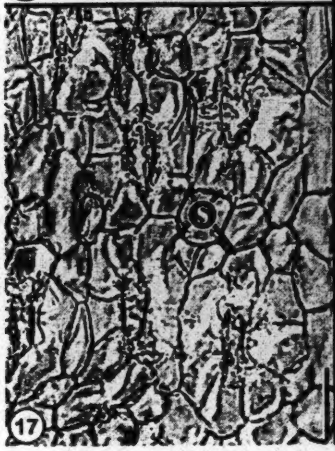
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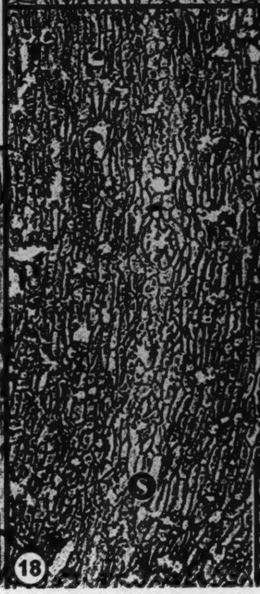
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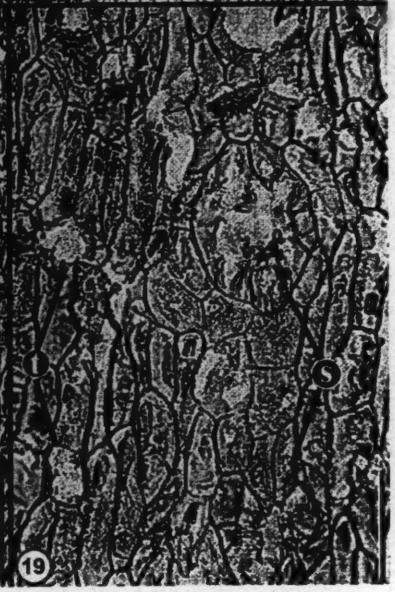
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Figs. 20-26. *Emporia lockardii* pollen cones. **20**. Mature ellipsoidal cone attached to ultimate shoot with slightly-concave leaves. M 3998, scale bar = 7 mm. **21**. Mature cone with ultimate shoot attached at base. M 998, scale bar = 5 mm. **22.** Mature cone with widely spaced microsporophylls. M 1823, scale bar = 5 mm. **23**. Mature cone showing large microsporophylls. M 2762, scale bar = 5 mm. **24**. Macerated immature cone showing microsporophylls and adaxial pollen sacs on microsporophyll shank (arrowhead). M 2906, scale bar = 2 mm. **25.** Immature cone showing ellipsoidal shape, helically arranged microsporophylls, and ultimate shoot at base. M 3047, scale bar = 5 mm. **26**. Immature cone. M 2903, scale bar = 2 mm.

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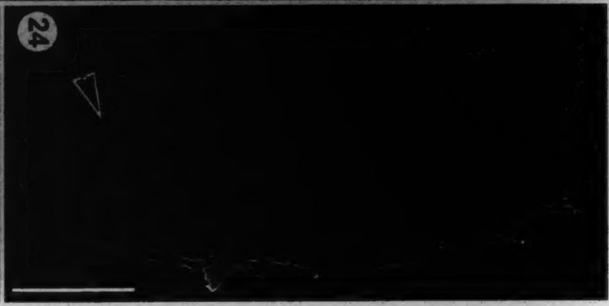
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Figs. 27-28. *Emporia lockardii* leaf from ultimate shoot attached to pollen cone. **27**. Ultimate leaf showing ellipsoidal shape and two broken adaxial bands of stomata (arrowheads). M 1823-6, scale bar = 1 mm. **28**. Adaxial stomatal band showing stomatal complexes (s) and several epidermal cell in between (brackets). M 1823-6, scale bar = 0.5 mm.

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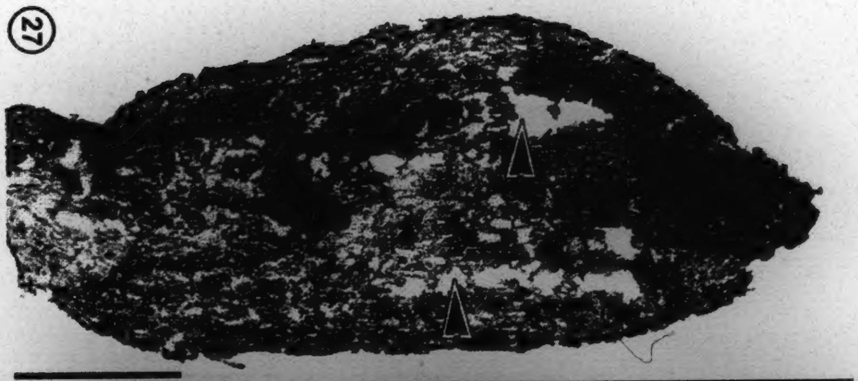

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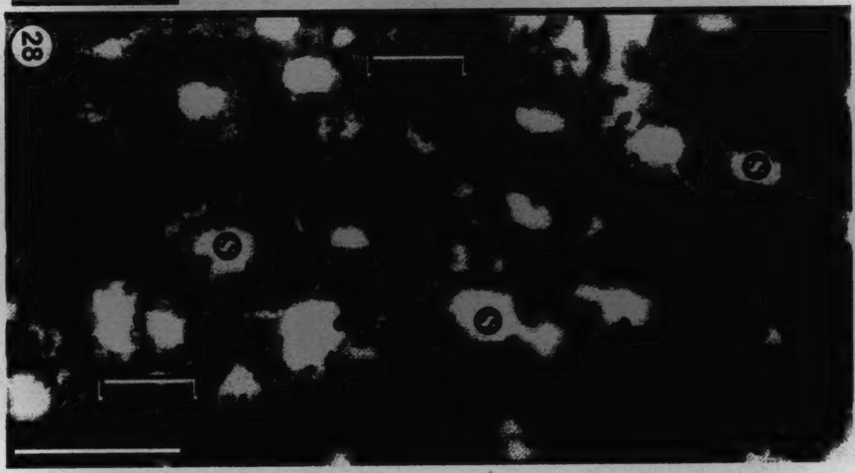
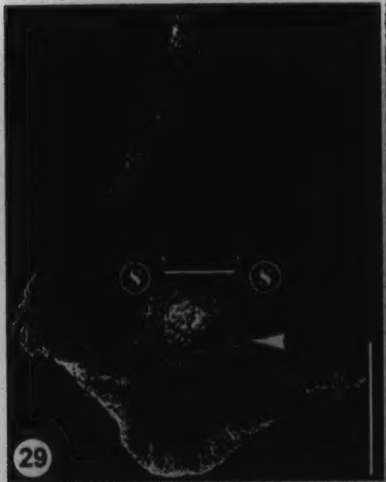


Figs. 29-35. *Emporia lockardii* SEM of microsporophylls and *Potonieisporites* prepollen grains. Specimens macerated from M 2906. **29**. Adaxial surface showing triangular shape, two major bands of stomata (s) separated by stomatal free zone (bracket), and remnants of shank (arrowhead). Scale bar = 1 mm. **30**. Three adaxial bands of stomata with papillate subsidiary cells (s), papillate epidermal cells, and elongated epidermal cells in stomatal free zone (bracket). Scale bar = 200 μm. **31.** Adaxial stomatal band showing circular to slightly ellipsoidal stomatal complexes with erect to overarching papillae. Scale bar = 20 μm. **32.** Abaxial surface entirely covered by trichome bases. Scale bar = 1 mm. **33.** Abaxial trichome bases. Scale bar = 40 μm. **34**. Internal view of abaxial surface with trichome bases and elongated epidermal cells (bracket). Scale bar = 40 μm. **35**. Distal view of two prepollen grains. Scale bar = 20 μm.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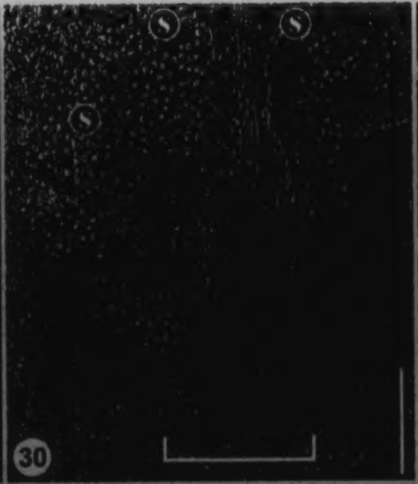
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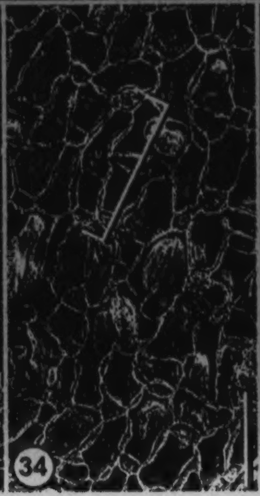
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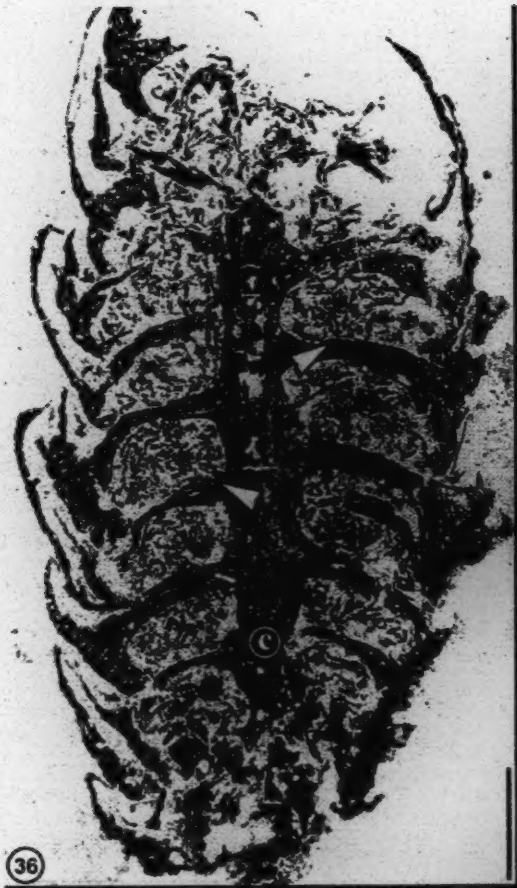
Figs. 36-40. *Emporia lockardii* anatomy of pollen cones and *Potonieisporites* prepollen grains. **36**. Radial section of ellipsoidal cone showing cone axis (c), peltate microsporophylls with attached adaxial pollen sacs (arrowheads). M 196-2, scale bar = 1 mm. **37**. Radial section showing microsporophylls with attached adaxial pollen sacs (arrowheads). M 196-2, scale bar = 1 mm. **38.** Cross section showing cone axis (c), helically arranged microsporophylls, and adaxial pollen sacs (arrowheads). M 157-6, scale bar = 1 mm. **39**. Microsporophylls showing stalk with adaxial pollen sacs (arrowheads). M 157-6, scale bar = 0.5 mm. **40**. Distal view of *Potonieisporites* prepollen. M 157-5, scale bar = 20 μm.



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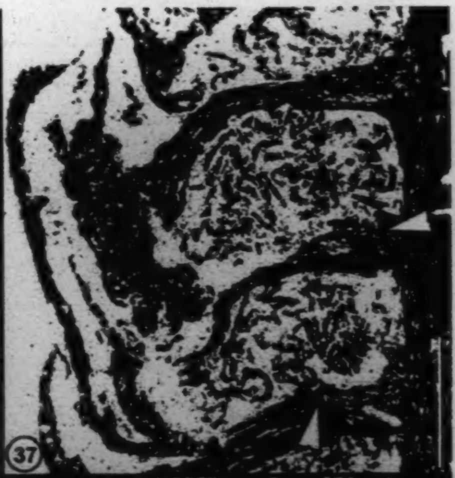

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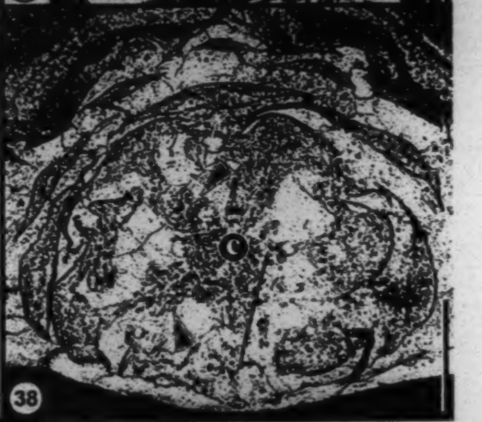

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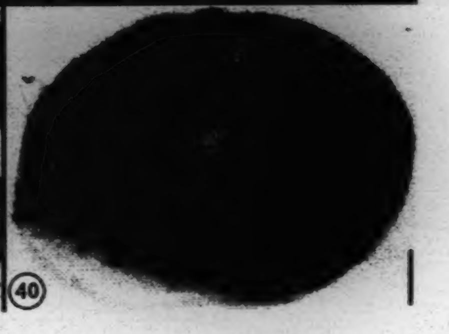

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Figs. 41-42. *Emporia lockardii* ovulate cones. **41**. Mature cone on penultimate shoot with leaves at base (arrowhead). M 608 A, scale bar = 1 cm. **42**. Incomplete cone showing cone axis (c), bract (arrowhead), and axillary dwarf shoot (bracket). M 2963 E, scale bar = 5 mm.

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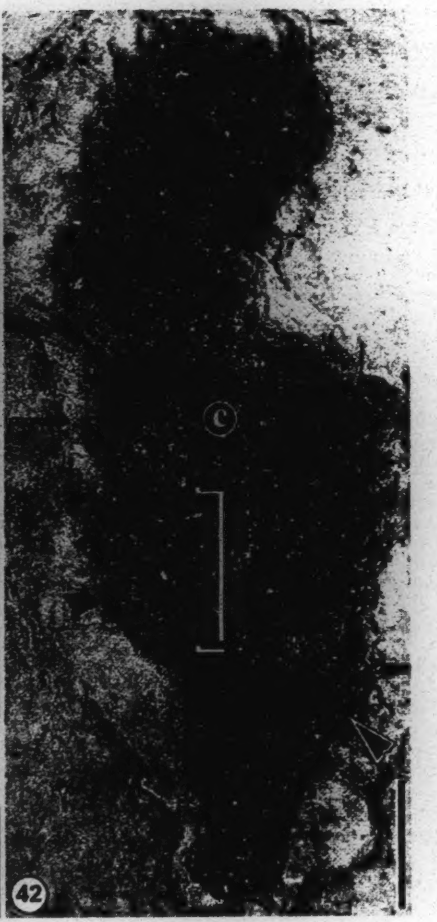

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Figs. 43-47. *Emporia lockardii* SEM of sterile scales and megasporophylls. All specimens macerated from M 1625. **43**. Adaxial surface showing lanceolate shape, marginal trichomes, and two broad bands of stomata (s). Scale bar = 1 mm. **44**. Abaxial surface showing ellipsoidal shape and trichome bases. Scale bar = 1 mm. **45**. Abaxial surface showing widely obovate shape and trichome bases. Scale bar = 0.5 mm. **46.** Adaxial surface of megasporophyll showing area of sub-apical seed scar (sc). Scale bar = 0.5 mm. **47**. Abaxial surface of megasporophyll showing raised central area and numerous circular trichome bases. Scale bar = 0.5 mm.

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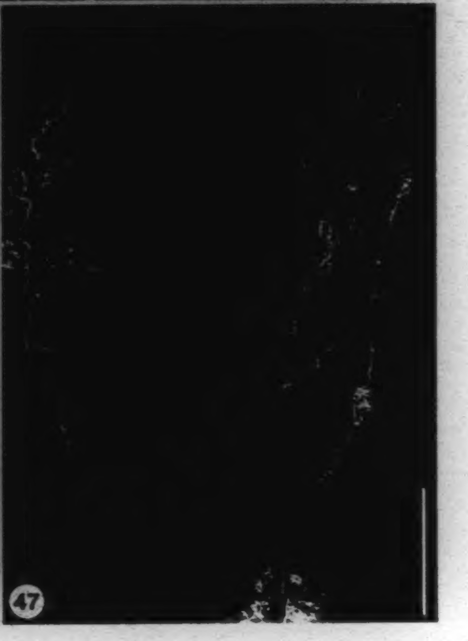
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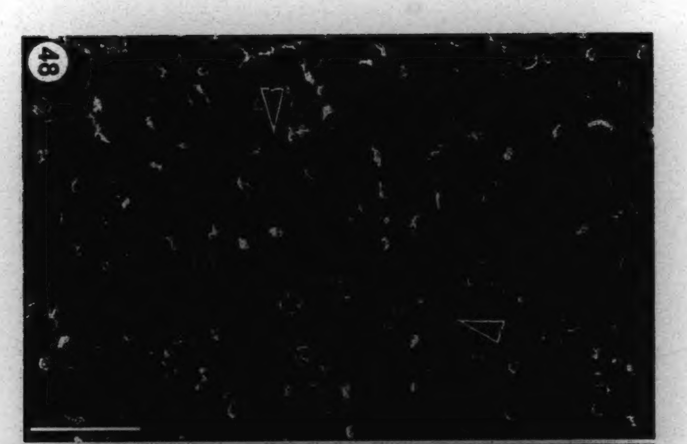
Figs. 48-50. *Emporia lockardii* SEM of cuticular features of sterile scale. All specimens macerated from M 1625. **48**. Adaxial band of stomata with numerous stomata encircled by papillate subsidiary cells (at arrowheads). Scale bar = 50 μm. **49**. Adaxial stomatal complexes with overarching papillae. Scale bar = 20 μm. **50.** Abaxial trichome bases (arrowheads). Scale bar = 20 μm.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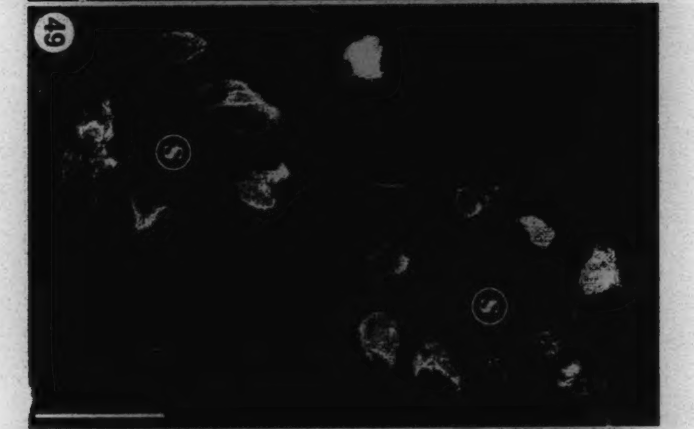
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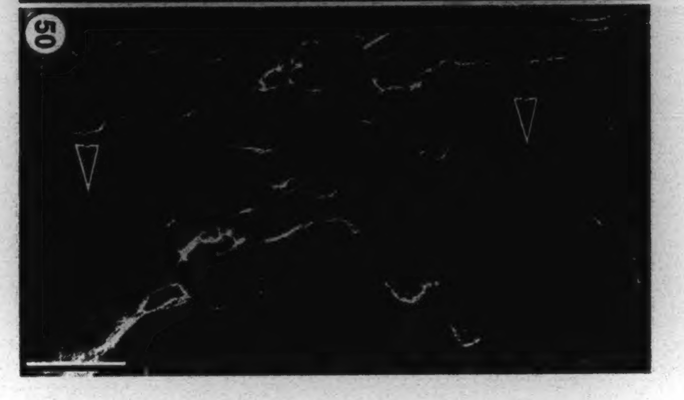
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CHAPTER 4

The whole plant reconstruction of *Emporia cryptica sp. nov.* (Voltziales: Emporiaceae) from the Hamilton Quarry, Kansas, USA.

1. Introduction

The fossil record of conifers extends back to the Upper Carboniferous (Pennsylvanian) and Early Permian (Rotliegendes ≈ Autunian) sediments of Euramerica (Florin 1938-45; Galtier et al., 1992; Rothwell et al., 1997). These Euramerican conifers are classified in several families within the Voltziales (Florin, 1938-45; Visscher et al., 1986; Kerp et al., 1990; Mapes and Rothwell, 1991), and are commonly referred to as walchian conifers (Mapes and Rothwell, 1984). Plants are often preserved as isolated and/or fragmentary lateral branches, and pollen and ovulate cones, usually in localities where more than one conifer has been preserved (Florin, 1938-45; Rothwell, 1982; Clement-Westerhof, 1984, 1987; Mapes and Rothwell, 1984, 1991, 1998; Meyen, 1984; Kerp, et al., 1990). The first and most crucial systematic work on these walchian conifers was proposed by Florin (1927, 1938-45, 1950, 1951), who correlated vegetative and reproductive remains by means of morphological and cuticular analyses and proposed the first systematic relationships among Paleozoic conifers and the origin of the conifer cones.

Florin's interpretations remain as some of the most influential for living and fossil conifers (Florin, 1938-45, 1951). Nevertheless, modern studies have questioned Florin's systematics and interpretations of the most primitive conifers (Schweitzer, 1963; Rothwell, 1982; Clement-Westerhof, 1984, 1987, 1988; Mapes and Rothwell, 1984, 1991, 1998; Meyen, 1984, 1997; Winston, 1984; Visscher, et al., 1986; Kerp, et al., 1990; Kerp and Clement-Westerhof, 1991; Hernandez-Castillo, et al., 2001a, 2001b). These new interpretations have been summarized by Hernandez-Castillo et al. (2001b) and a complete reevaluation and reexamination was proposed for these ancient conifers employing new methodologies and reliable criteria for circumscribing species of walchian conifers as complete plants. This approach is based on a combination of morphological, cuticular, and anatomical characters that are used to correlate vegetative branches with pollen and ovulate cones. In the current study we employ this approach to reconstruct *Emporia cryptica* sp. nov. (Emporiaceae) from the Late Pennsylvanian Hamilton Quarry, Kansas, USA. This reconstruction is part of broader study to reinvestigate, describe and reevaluate morphological characters and to reconstruct Paleozoic walchian conifers as complete plants, so they can be used to resolve systematic relationships among fossil and living conifers.

2. Material and Methods

2.1 Material

The specimens used in this study are preserved as coalified compressions with preserved cuticles and cellular permineralizations. They occur in Late Pennsylvanian laminated carbonate mudstones of the Hartford Limestone, Topeka Limestone Formation, Shawnee Group, located east of Hamilton, Kansas, USA (Fig. 1: Mapes and Rothwell, 1984; Bridge, 1988; French et al., 1988; Busch, et al., 1988). These beds represent channel deposits in an estuarian environment under tidal influence (French et al., 1988; Fahrer, et al., 1990; Fahrer, 1991; Feldman et al., 1990, 1993). The Hamilton Quarry yields an exceptionally well-preserved and diverse biota that includes bryozoans, crinoids, fusulinids, marine microinvertebrates, non-marine bivalves, eurypterids, crustaceans, ostracods, millipedes, insects, sharks, fish, amphibians, reptiles, and a rich terrestrial flora (Mapes and Mapes, 1988; Rothwell and Mapes, 1988, 2001; Fahrer et al., 1990; Fahrer, 1991; Feldman et al., 1993). *Emporia cryptica* is represented by 157 specimens. Thirty three of these are plagiotropic, leafy branching systems with penultimate and ultimate shoots attached, and four have cuticles preserved. Seventy one are pollen cones; 14 of them are attached to ultimate shoots; 14 have cuticles preserved; and 10 are anatomically preserved. Fifty-three are ovulate cones, eight of them attached to penultimate shoots with leaves; 11 have cuticles preserved, and four are anatomically preserved.

2.2 Methods

Specimens were initially revealed on split surfaces of the limestones. Cuticles were macerated from the matrix with dilute (0.5-1%) HCl, rinsed in distilled water, bleached in Lysol toilet bowl cleaner (Reckitt Benckiser, Toronto, Canada), allowed to air dry on microscope slides, and mounted under a cover slip with Eukitt (O. Kindler GmbH Co., Freiburg, Germany). For scanning electron microscopy cuticles were air dried on specimen stubs and coated with (100 Å) gold, and examined on a JEOL (Japan Electron Optics Ltd.) 6301 FXV and a Phillips XL30 ESEM (FEI Co., Tokyo, Japan) scanning electron microscopes. Some anatomically preserved specimens were prepared with the cellulose acetate peel technique (Joy et al., 1956), and others were cut into wafers and ground thin enough to transmit light. Compressed specimens with some anatomical preservation were etched with 1-5% HCl, flooded with acetone, and a cellulose acetate peel was placed on the split surface. These surface pulls were removed while the acetate was still plastic enough to be pressed relatively flat under a heavy weight. Light microscopy was conducted using Zeiss Ultraphot IIIB and WL microscopes, and images captured with a MicroLumina digital scanning camera (Leaf Systems Inc., Bedford, MA) or a PhotoPhase digital scanning camera (Phase One A/S, Frederiksberg, Denmark). Images were processed using Adobe Photoshop. All specimens are housed in the Ohio University Paleobotanical Herbarium, Athens, Ohio, USA.

3. Results

3.1 Systematics. –

Class – Coniferopsida

Order – Voltziales

Family – EMPORIACEAE Mapes et Rothwell

Genus - ***Emporia*** Mapes and Rothwell, 2003.

Species - *Emporia cryptica* Hernandez-Castillo, Stockey, Mapes et Rothwell, **sp. nov.** (Figs. 1-72).

Holotype. Penultimate shoot with attached ovulate cone. Specimen M 1613, figures 45-49, 63-64, 70-72.

Paratypes. Branches showing leaf morphology on penultimate and ultimate shoots M 2789A, M2789B, M 3004C, M 4013, M 233, M760 (Figs. 2-7). Cuticles on leaves of penultimate shoots and ultimate shoots M 2970, M 1279 (Figs. 8-21). Pollen cones M 1061, M 2904, M 1055, M 3010 (Figs. 22-25). Vegetative leaves of ultimate shoots attached to pollen cones M 170-2, M1823-6 (Figs. 26, 27). Pollen cone macerations and pollen M 1625 (Figs. 28-33). Anatomically preserved pollen cones M 170 (Figs. 34-40). Ovulate cones M 1642A, M 1399, M 1602 (Figs. 41-43). Cuticles of ovulate cones M 2983, M 1613, M 2970, M 2978A (Figs. 44-60). Anatomy of ovulate cones M 1613, M 2983B, M 2984B (Figs. 61-75).

Collecting locality. Hamilton Quarry; NW quarter, sec. 5 and 8, T.24S., R.12E., Virgil seven and a half foot quadrangle, Greenwood County, Kansas, U.S.A. Figure 1.

Stratigraphic occurrence and age. Hartford Limestone, Topeka Limestone Formation, Shawnee Group, Late Pennsylvanian.

Etymology. The specific epithet *cryptica* refers to the cryptic nature of individual characters of the plant organs when organ by organ comparison is done without a complete plant approach.

Diagnosis. Characters of species those of genus. Leaves on penultimate shoots simple to forked, narrowly triangular to linear (face view), slightly concave to spreading (side view), 2.4-7.1 mm long, 0.6-1.2 mm wide. Leaves on ultimate shoots narrow, triangular to linear (face view), slightly S-shaped to slightly concave (side view), 1.2-2.7 mm long, 0.3-1.2 mm wide. Epidermal cells rectangular, elongate to polygonal, often unipapillate; marginal trichomes present, short and long. Adaxial stomatal bands, two, separated by elongate epidermal cells. Stomata monocyclic, 53 x 44 μm in diameter, 5-8 unipapillate subsidiary cells, guard cells sunken; dicyclic stomata scattered. Adaxial trichome bases few to abundant. Abaxial stomatal bands, two to three, narrow. Abaxial trichome bases abundant. Pith resin rodlets elongate. Secondary xylem tracheids multiseriate, bordered pits circular to hexagonal; wood rays 1-3 cells high. Pollen cones cylindrical to ellipsoidal, 1.4-4.7 cm long, 0.8-2.9 cm wide. Microsporophylls 0.5-4.5 mm long, 1.9-2.7 mm wide. Pollen sacs 4-8, adaxial, ellipsoidal, attached to single area on shank. Microsporophyll distal lamina with two adaxial stomatal bands; stomata 25-45 x 35-54 μm, 5-7 unipapillate subsidiary cells; epidermal cells unipapillate. Prepollen of *Potonieisporites* type, subcircular to ellipsoidal in polar view, 100-112 μm wide, 70-80 μm long. Leaves on ultimate shoots subtending pollen cones like those on vegetative ultimate shoots. Ovulate cones ellipsoidal, 3.0-8.6 cm long, 1.2-1.9 cm wide. Bracts forked with cuticular features like those of forked leaves on penultimate shoots. Axillary ovuliferous dwarf shoots fused at base. Sterile scales linear to widely obovate, apex mucronate to mucronulate, up to 25, 1.5-3.2 mm long, 0.7-3.2 mm wide, amphistomatic. Sporophylls narrow, two, covered by numerous trichome bases. Ovules bilateral, flattened, winged; base rounded to subcordate. Ovule attachment scar basal to sub-lateral; nucellus fused except at micropyle; nucellar beak present; pollen chamber simple. Embryos polycotyledonary.

4. Description

4.1 Branching Systems

The specimens consist of three orders of branching with an antepenultimate shoot that bears several lateral plagiotropic branches (Figs. 2, 3). These lateral branches are composed of a leafy penultimate shoot with attached ultimate leafy shoots (Figs. 2-7). Some branches may show slightly irregular branching (Fig. 6). Branch shape ranges from deltoid (Figs. 2-4, 7) to narrowly oblong (Fig. 5). The largest plagiotropic branch measures 15 cm long and 7.9 cm wide (Fig. 4). The longest ultimate shoots (ca. 4.2 cm long) occur in the mid-region of large branches (Fig. 4), while the shortest (1.9 cm long) occur on small narrowly oblong branches (Fig. 5). Most lateral branches are broken at the very base or the apex (Figs. 2-7) indicating that some plagiotropic shoots were larger than the specimens shown here. Penultimate shoots range 0.1-4.0 mm in diameter.

4.2. *Leaves on penultimate shoots*

Leaves are simple, helically arranged, 2.4-7.1 mm long and 0.6-2.0 mm wide (Figs. 1-7). They are narrowly triangular with a broad base in face view (Figs. 8-11) and slightly S-shaped and spreading (extending nearly to the horizontal) in side view (Figs. 5, 7) with numerous marginal trichomes (Figs. 8-11). They diverge at almost 135° and then they curve towards the apex of the branch at an angle of 45° (Figs. 5, 7). Cuticular macerations yield dark-colored leaves (Figs. 8-14) in which stomatal bands are often difficult to see (Figs. 8, 10). Closer examination of these leaves reveal two adaxial bands of stomata (Figs. 10, 13) and numerous dicyclic stomata ("dark spots") on the leaf surface (Figs. 10-12). Stomata are ellipsoidal, 28-42 μm wide, 62-78 (-104) μm long and have 5-6 subsidiary cells with overarching papillae (Fig. 13). Individual stomata are close to each other and sometimes share adjacent subsidiary cells (Fig. 13). Bands are separated by a stomatal free zone of polygonal to rectangular epidermal cells. Most regular epidermal cells in marginal and stomatal free zones display small erect papillae (Fig. 12). Semicircular dicyclic stomata, 42-73 μm wide, 57-88 μm long, with unipapillate subsidiary cells are scattered on the entire adaxial surface (Figs. 10-12). The abaxial surface is completely covered by surficial trichome bases and has two narrow bands of stomata (Fig. 14). These bands are 2-3 stomata wide with 6-7 subsidiary cells and a single overarching papilla (Fig. 14). The leaf margin has both short and long trichomes (Figs. 8-11).

4.3. Leaves on ultimate shoots

Leaves are slightly concave to slightly S-shaped and spreading in side view (Figs. 4-7), and narrow sub-triangular to linear in face view (Fig.15). They are 1.2-2.7 mm long and 0.3-1.2 mm wide, and diverge from the stem at 26-63° at the base and 28-69° at the apex of the shoot. Leaves are amphistomatic, with two long bands of adaxial stomata separated by a stomatal free zone (Figs. 15-16). Leaf margins and stomatal free zones have rectangular, longitudinally elongate epidermal cells with abundant papillae and trichome bases (Fig. 16). Marginal trichomes are often short or broken (Figs. 15, 16, 18). Stomatal complexes are in contact with each other and usually share subsidiary cells (Figs. 16, 19). Stomata are monocyclic, ellipsoidal to semicircular, 53 x 44 μm, and have 5-8 subsidiary cells with overarching papillae (Figs. 16). Dicyclic stomata are found on large leaves (Fig. 18), and both inner and outer cycles have unipapillate subsidiary cells (Fig. 19). The abaxial surface shows two narrow bands of stomata (Figs. 20-21) that have five to six unipapillate subsidiary cells (Fig. 21). The entire abaxial surface is covered by trichome bases that are circular at the base and surrounded by elongate epidermal cells (Fig. 21).

4.4. Pollen cones

4.4.1. Morphology of pollen cones

Pollen cones are simple, terminal, ellipsoidal, and 1.4-4.7 cm long, 0.8-2.9 cm wide (Figs. 22-25). Cones bear helically arranged microsporophylls, 0.5-4.5 mm long, 1.9-2.7 mm wide (Figs. 22-25). Microsporophylls have a narrowly triangular distal end, broad base, and are attached to the cone axis by a shank (Figs. 22-25). Pollen cones are often in organic connection with ultimate shoots that bear leaves (Figs. 22, 24), but many of them are isolated or broken (Figs. 23, 25). Leaves on these shoots are simple (Figs. 26) and similar to those of penultimate shoots (Table 1). They have two bands of stomata separated by a stomatal free zone (Fig. 26) and stomatal complexes have unipapillate subsidiary cells (Fig. 27). Leaf margins and stomatal free zones have rectangular epidermal cells and abundant papillae and trichome bases (Fig. 27).

4.4.2. Cuticular features of microsporophylls

Microsporophylls yield cuticles showing two broad bands of adaxial stomata, surficial trichome bases, papillae, and marginal trichomes (Figs. 28-33). Bands are separated by a stomatal free zone with numerous unipapillate epidermal cells (Fig. 30). Stomata are ellipsoidal to semicircular, 25-45 μm wide x 35-54 μm long, with 5-7 unipapillate subsidiary cells (Figs. 30-31). Papillae on subsidiary cells are often erect (Fig. 31). The abaxial surface is completely covered by surficial trichome bases that are often broken (Figs. 32, 33).

4.4.3. Anatomy of pollen cones and prepollen

Pollen cones have a cone axis bearing helically arranged peltate microsporophylls (Fig. 34). Four to eight, abaxial, ellipsoidal, pollen sacs are attached to a single area on the shank (Figs. 35-37). Many pollen sacs are empty (Figs. 35-37), but some are full of monosaccate prepollen grains that conform to the *sporae dispersae* genus *Potonieisporites* Bharadwaj (1964) (Fig. 38). Grains are subcircular to ellipsoidal with a large saccus that surrounds a central body (Figs. 38-40). This central body has a proximal bent monolete suture and parallel fold that is often broken (Figs. 38-40). Grains are 100-112 μm wide, 70-80 μm long in polar view.

4.5. Ovulate cones

Cones are ellipsoidal, 3.0-8.6 cm long, 1.2-1.85 cm wide and bear several helically-arranged bracts and axillary ovuliferous dwarf shoots (Figs. 41-43). These cones can be differentiated from other *Emporia*-like cones in the locality due to their long and slender overall appearance (Figs. 41, 42), and the presence of axillary dwarf shoots that are as long as the subtending bracts (Figs. 41, 43). Axillary dwarf shoots diverge from the cone axis at 45-90° angles and have 20-25 sterile scales (Figs. 41, 43). Sporophylls are often difficult to see unless the cone is macerated. Many ovulate cones are in organic connection with penultimate shoots (Figs. 41-43). Leaves on these shoots are simple (Figs. 42- 43) and similar to those found on penultimate shoots (Table 1).

4.5.1. Bracts

Bracts are forked and have a broad base with numerous marginal trichomes (Fig. 44-45). They have numerous adaxial dicyclic stomata (Figs. 46-48), like leaves on vegetative shoots. The adaxial surfaces have two bands of stomata, one per forked tip (Fig. 44). Stomata are ellipsoidal to semicircular and have 6-8 papillate subsidiary cells with overarching papillae (Fig. 47). Dicyclic stomata are scattered on the entire adaxial surface (Fig. 47) and have unipapillate subsidiary cells (Fig. 48). Leaf margins and stomatal free zones have rectangular epidermal cells with numerous papillae and trichome bases (Figs. 47-48). The abaxial surface has two narrow bands of stomata and is entirely covered by trichome bases (Fig. 49).

4.5.2. Sterile scales

Sterile scales are narrowly subtriangular, triangular to ovate with mucronate apex (Figs. 50, 51, 54, 55). They are 1.5-3.2 mm long and 0.7-1.2 mm wide. Scales are amphistomatic with narrow bands of stomata (Figs. 50-53). The adaxial surface has two stomatal bands, while the abaxial surface may have up to three narrow bands (Figs. 50, 51). Stomatal complexes have 7-8 papillate subsidiary cells (Fig. 52, 53). Leaf margins and stomatal free zones have rectangular epidermal cells with numerous papillae and trichome bases (Figs. 52, 53).

4.5.3. Sporophylls and ovules/seeds

Sporophylls are narrow, 1.1-1.9 mm long, 0.6-0.8 mm wide with a sub-apical seed scar. They are completely covered by trichome bases (Fig. 58). Ovules/seeds are bilateral, flattened, with rounded to subcordate bases, small wings, and covered with short uniseriate trichomes that are often broken (Fig. 60).

4.6. Internal anatomy

4.6.1. Stem

Stems have a parenchymatous pith with patches of cells with dark contents that may represent secretory substances (Fig. 58). Pith parenchyma cells are more-or-less rectangular, longitudinally aligned, and axially elongated (Fig. 59). Primary xylem tracheids have helical or scalariform secondary wall thickenings (Figs. 58-60). Tracheids of the secondary xylem have multiseriate hexagonal bordered pits on the radial walls (Figs. 58, 61). Wood rays are uniseriate,1-3 cells high (Fig. 62). The outer cortex is poorly preserved and no clear vascular cambium, phloem or periderm can be accurately identified. However, rectangular to polygonal, thin-walled cells that may have dark contents have been observed in the outer cortex, and are similar to those found in the pith. Epidermal cells are rectangular in longitudinal section and are covered by a thick cuticle.

4.6.2. Ovulate cones

The woody cone axis bears bracts that subtend axillary dwarf shoots with inverted seeds (Figs. 63-64). The bract and dwarf shoot diverge as a single unit, but separate almost immediately after diverging from the cone axis (Fig. 62, upper right). Ovuliferous dwarf shoots extend from the axis at 45°-90°. Axillary dwarf shoots have 20-25 sterile scales on all surfaces but concentrated on the abaxial surface at the shoot apex (Figs. 61-62).

4.6.3 Ovules/seeds

Ovules are bilaterally symmetrical, ovoid to ellipsoidal, 2.4-7.0 mm long, 1.4-1.8 mm wide and inverted where the micropyle faces the cone axis (Figs. 63-67, 70-72). Each ovule has two wings (Figs. 65, 66). The sarcotesta is single-layered, while the sclesrotesta is composed of several layers of thick-walled cells (Figs. 65-67). The endotesta is typically single-layered but up to three layers of cells have been observed in some sections (Figs. 65-68, 70). There is no direct evidence of vascular tissue in the integument. The nucellus is a single layer of cells and free from the integument except at the micropylar end and shows a nucellar beak (Figs. 65-68, 70). The pollen chamber sometimes contains monosaccate *Potoniesporites* prepollen grains that appear to have a substance surrounding them that changes the optical properties of the slides (Figs. 67-70).

A single cone yielded mature seeds where integuments, nucellus, megaspore membrane, megagametophyte, and polycotyledonary embryos are preserved (Fig. 71, 72; also Fig. 7E, Mapes and Rothwell, 1988; Fig. 1b, Mapes et al., 1989). Six seeds have embryos preserved, four of which have cellular megagametophytes and embryos (Figs. 70-72). Six cotyledons have been observed in the most mature seeds (Fig. 7E, Mapes and Rothwell, 1988; Fig. 1b, Mapes et al., 1989). The embryo is separated from the megagametophyte by a narrow corrosion cavity (Fig. 72; Fig. 1b, Mapes et al., 1989). A few cells that resemble tracheids are present in the center of the embryo and may represent the procambium (Fig. 1b, Mapes et al., 1989).

5. Discussion and conclusions

5.1. *Emporia cryptica*

Emporia cryptica conforms to the general architecture recently determined for walchian conifers (Lausberg, 2002; Hernandez-Castillo et al., 2003). These were relatively small plants with orthotropic stems from which plagiotropic lateral branches of determinate growth produce terminal pollen and ovulate cones. Among primitive conifers, *E. cryptica* has a novel combination of characters that include 1) two orders of branching (penultimate and ultimate shoots), 2) multiseriate hexagonal bordered pits on secondary xylem tracheids, and 3) resin rodlets with axially aligned secretory cells in the pith. 4) simple needle-like leaves on penultimate and ultimate branches (i.e., lacks heterophylly), 5) amphistomatic leaves with two broad adaxial and two narrow abaxial bands of stomata, 6) dicyclic stomata on the adaxial surface of all leaves and leaf-like structures, 7) simple, terminal pollen cones, 8) peltate microsporophylls with adaxial pollen sacs, 9) monosaccate prepollen grains, 10) compound ovulate cones that bear bracts and ovuliferous dwarf shoots, 11) bracts and ovuliferous dwarf shoots fused at the base but separated distally, 12) bracts forked, 13) bilaterally symmetrical ovuliferous dwarf shoots with interspersed sterile scales and sporophylls, 14) sterile scales up to 25 per dwarf shoot, 15) sporophylls two per dwarf shoot, narrow and slightly recurved at apex, 16) one inverted, winged ovule per sporophyll, 17) simple pollen chamber, 18) nucellar beak present, 19) embryos with up to six cotyledons.

Although almost all of these individual characters occur in other previously described walchian conifers (Florin, 1938-45; Mapes and Rothwell, 1984; Kerp et al., 1990; Hernandez-Castillo et al., 2001b; Rothwell and Mapes, 2001; Rothwell et al., 2005; chapter 3 in this dissertation;), *Emporia cryptica* displays a novel combination of characters that is not known for any of the previously described species of Paleozoic conifer plants (Table 1). Among these characters, the presence of dicyclic stomata, multiseriate hexagonal circular bordered pits, and axially arranged secretory cells are distinct characters that make this plant unique among previously described species.

Other species of walchian conifers have dicyclic stomata (Florin 1938-45; Clement-Westerhof, 1984, 1987), incompletely dicyclic stomata (Florin, 1938-45; Kerp et al. 1990), uniseriate to biseriate circular (Galtier et al., 1992; Hernandez-Castillo et al., 2001b; Mapes and Rothwell 2003) or hexagonal bordered pits (Florin, 1938-45, plate 159-160, figs., 19-21), or resin rodlets (secretory cells) like those of *E. cryptica* (Mapes and Rothwell, 1984; Rothwell and Mapes, 2001) but none of these taxa displays the same combination of characters seen in *E. cryptica*.

5. 2. Systematic relationships

Comparisons of *Emporia cryptica* to Euramerican Voltziales at the whole plant level are more meaningful than comparisons to individual morphotaxa due to the overlapping variation of morphological and cuticular characters of individual organs within a single conifer and (Tables 1-5; Hernandez-Castillo et al., 2001b; Rothwell et al., 2005; chapter 3 in this dissertation). *Emporia cryptica* reveals another novel combination of characters and is now added to a growing list of studies of complete conifer reconstructions (Hernandez-Castillo et al., 2001b; Rothwell and Mapes, 2001; Rothwell et al., 2005; chapter 3 in this dissertation). Comparisons between *E.* cryptica and the most complete and most similar Euramerican walchian Voltziales are summarized in Table 2. Among these taxa, only *Thucydia mahoningensis* Hernandez-Castillo, Rothwell & Mapes and *Ernestiodendron filiciforme* Florin share the same suite of characters for vegetative lateral branches and pollen cones (Table 2). This suite of characters includes plagiotropic lateral branches with simple leaves on both penultimate and ultimate shoots and a lack of heterophylly (Table 2). However, *T. mahoningensis* differs from *E.* cryptica in having primarily adaxial stomata, no abaxial stomata, a fertile zone instead of a cone with 3-4 sporophylls per dwarf shoot, and a compound pollen cone (Table 2). *Ernestiodendron filiciforme* differs from *E. cryptica* by having parallel rows of adaxial and abaxial stomata, bracts and axillary dwarf shoots that are completely separate throughout, and a single sporophyll per dwarf shoot (Table 2).

The most similar species to *E. cryptica* are *Emporia lockardii* (Mapes and Rothwell) Mapes and Rothwell and *Otovicia hypnoides* (Florin) Kerp, Swinkels, & Verwer (Table 2). Both have amphistomatic leaves with two bands of adaxial stomata, and ovulate cones with interspersed terminal sporophylls like *E. cryptica* (Table 2). However, they differ by having age- or position-dependent heterophylly, abaxial stomata in short bands or individual rows, or scattered, and bracts and axillary dwarf shoots that are separate even at the base (Table 2). Both *E. lockardii* and *O. hypnoides* have sporophylls interspersed with sterile scales, as in *E. cryptica,* but only *O. hypnoides* shares the same number of sporophylls per axillary dwarf shoot (Table 2). Number of sporophylls per dwarf shoot falls within the variation seen in *E. lockardii* (Table 2), suggesting a close affinity to that species.

5.3. Characters in walchian conifers

Morphological characters of leaves on penultimate and ultimate shoots were traditionally used to typify walchian conifer species (i.e., Florin 1927, 1938-45; Clement-Westerhof, 1984; Visscher et al., 1986). Unfortunately, leaves have some of the most overlapping characters among walchian conifers (Tables 1, 3; Hernandez-Castillo et al., 2001b, chapters 3 and 5). For example, leaves may range from narrowly triangular or sub-triangular to linear (in face view) and slightly S-shaped to slightly concave and spreading (in side view), regardless of their position on lateral branches (Tables 1, 3). Size of the leaves on ultimate shoots overlaps considerably among species from different genera and families (Table 3), and is one of the most used characters to differentiated species when cuticles are not available (Florin 1938-45). Angles of divergence of leaves on ultimate shoots are may vary greatly from species to species or they may be almost the same in taxa from different families (Table 3). Given this, it is obvious that the practice of only using these characters to identify isolated and fragmentary walchian conifer remains is flawed (Table 3; Hernandez-Castillo et a., 2001b, chapter 2).

Cuticular characters of leaves from ultimate shoots are also often used to differentiate among genera and species of walchian conifers (see Hernandez-Castillo et al., 2001b). These characters may be useful to differentiate distinctive conifers such as *Ernestiodendron* or *Hanskerpia* from other walchians such as *Otovicia* or *Utrechtia*, but they overlap so much that their use when describing isolated or fragmentary material will undoubtedly bias the results (Tables 1, 4). Most conifers described so far have amphistomatic leaves with two bands of stomata and stomata with similar number of subsidiary cells, trichome bases and papillae on epidermal cells (Table 4). Among these, patterns of stomatal distribution, stomatal complex structure, number of stomata per band, and number of subsidiary cells are shared by these conifers (Tables 1, 4). However, characters such as subsidiary cell number need to be explored in more detail in all orders of leaves and leaf-like structures (i.e., bracts and sterile scales) of a complete plant if they are to be used as proxies to differentiate fragmentary walchian conifers (Table 1). The assumption that all cuticles on a single walchian conifer plant are the same is, at best, misguided (Table 1; Hernandez-Castillo, et al., 2001b, chapter 2). For example, *E. cryptica* has different numbers of subsidiary cells and stomata sizes on different branching orders of leaves and leaf-like structures (Table 1; Hernandez-Castillo, et al., 2001b, chapter 2).

Ovulate cone characters (Table 5), as in living conifer families, are used to differentiate walchian conifers and play an important role in their systematics (Florin 1938-45, 1950; 1951; Clement-Westerhof, 1984, 1987, 1988; Kerp et al., 1990; Kerp and Clement-Westerhof, 1991; Mapes and Rothwell, 1991, 2003; Hernandez-Castillo et al., 2001b; Rothwell and Mapes, 2001, 2003; Rothwell et al., 2005; chapter 3 in this dissertation). The presence of simple or forked bracts, bilateral or radial axillary dwarf shoots, the number of sterile scales per dwarf shoot, and the number and position (terminal or interspersed) of sporophylls are useful characters to distinguish species of walchian conifers where ovulate cones have been accurately described. However, good preservation and several cones are needed to account for all of these characters. Cone morphology must be combined with cuticular macerations to fully describe the material. Anatomical characters, when present, should be used to determine affinities and elucidate the reproductive biology of these plants. For example, *E. cryptica* can be distinguished using a combination of characters, and appears most similar to *E. lockardii* and *O. hypnoides* when the whole plant is reconstructed (Tables 2, 5). Although ovulate cone characters are helpful in distinguishing some species, attention needs to be paid to those characters on the rest of the plant to truly assess growth habit, taxonomy and phylogeny among walchian conifers (Hernandez-Castillo et al., 2001b, chapters 3 and 5).

5.4. Reproductive biology of Emporia cryptica

Due to the exceptional preservation at the Hamilton Quarry, numerous ovules and seeds can be seen at different developmental stages. As demonstrated by Mapes and Rothwell (1984), these developmental stages can be compared to those of living conifers when anatomical sections are available. The Hamilton Quarry conifers and *Moyliostrobus* *texanum* Miller et Brown are the only known permineralized ovules and seeds in Paleozoic conifers (Mapes and Rothwell, 1984, 1991; chapter 2).

The integument in young ovules of *E. cryptica* shows three layers of tissue (sarcotesta, sclerotesta, and endotesta) that are similar to those found in integuments of immature embryos of *E. lockardii*, *H. hamiltonensis*, (Mapes and Rothwell, 1984; Rothwell et al., 2005). The sarcotesta in *E. cryptica* forms the wing and is obvious in immature ovules but is reduced in mature seeds to a single layer (when present), and is covered by a thick cuticle with numerous trichomes similar to these of some extant conifers (Chowdhury, 1961; Mapes and Rothwell, 1984; Rothwell et al., 2005). The sclerotesta is composed of several layers of cells that are often broken and are full of dark contents suggesting that these seeds produced some sort of secretory substance in the integuments.

The nucellus in immature ovules has up to three layers of cells, but is often represented by a single layer of cells in mature ovules, and forms a nucellar beak, suggesting that *E. cryptica* has a similar nucellar maturation to that of living conifers (Chamberlain, 1935; Gifford and Foster, 1989). The pollen chamber shows a few prepollen grains inside that are surrounded by a substance (secretion?) that has a different refractive index to that of the ovule. Mapes and Rothwell (1984) hypothesized that the ratio between the open micropyles and diameter of prepollen grains in *E. lockardii* serve as indirect evidence of a pollination drop mechanism. A similar correlation has been found in *E. cryptica* where prepollen grains are rather large and it would be difficult for them to find their way into the micropyle using wind currents alone.

Thus, *E. cryptica* not only had seed dormancy (Mapes et al., 1989) but also a similar pollination mechanism to that seen in fossil *E. lockardii* and *O. hypnoides* as well as in living conifers with saccate pollen grains (Owens and Blake, 1983; Mapes and Rothwell, 1984; Owens et al., 1987; Owens and Morris, 1998; Kerp et al., 1990; Runions et al., 1999; Tomlinson and Takaso, 2002). Two types of pollination associated with saccate pollen grains are known among living conifers (Runions and Owens 1996; Runions et al., 1999; Tomlinson and Takaso, 2002). One of them involves inverted ovules and a pollination drop (Runions et al., 1999; Tomlinson and Takaso, 2002) and would be equivalent to the proposed pollination mechanism in *E. cryptica*, where an inverted ovule produces a pollination drop that aids prepollen grains to reach the pollen chamber during early stages of reproduction. The second type of pollination does not require a pollination drop and pollen reaches the micropyle by floating in rainwater (Runions and Owens 1996; Tomlinson and Takaso, 2002).

Immature, abortive, and mature ovules have been observed in *E. lockardii* and *H. hamiltonensis*, but no megagametophytes or embryos have been found in these conifers (Mapes and Rothwell, 1984; Rothwell et al., 2005). The only embryos previously reported (Mapes et al., 1989) are those now assigned to *E. cryptica* and these embryos (with up to six cotyledons) were published in two separate papers (Mapes and Rothwell, 1988, Figs. 7B, 7E; Mapes et al., 1989). Cellular megagametophytes of *E. cryptica* are the first known in Paleozoic conifers. In spite of the excellent preservation, no archegonia or early embryos have so far been found.

5.5. Conclusions

Emporia cryptica has a novel combination of characters that is unique among previously described species of walchian conifers. These were small stature conifer trees with lateral plagiotropic branches and terminal pollen and ovulate cones. *Emporia cryptica* is one the few complete fossil conifers where morphological and cuticular ranges of variation for both vegetative and fertile organs are known. Comparisons between *E. cryptica* and the best known "Walchian Voltziales" (Rothwell et al. 2005) show that many characters (i.e., morphology and leaf cuticles) commonly used to typify fossil conifers overlap considerably among species from different families. Even though individual and isolated or fragmentary conifer organs and their morphotaxon names may be important for preliminary floristic assessments (Lausberg and Kerp, 2000; DiMichelle et al., 2001), whole plants cannot be reconstructed unless good preservation and a large number of specimens is available. Only then can we appreciate relationships and understand the evolution of these conifers as extant species. *Emporia cryptica* extends our knowledge of the ranges of variation within a single walchian conifer and reinforces the idea that the most ancient conifers already possessed a similar reproductive biology to that of extant conifers. Previous whole plant conifer reconstructions and the present reconstruction of *Emporia cryptica* make the Hamilton Quarry the only locality in the world where four conifer species have been described as whole plants and the Emporiaceae the best known family of fossil conifers from Euramerica.

Table 1. Comparison of morphological and cuticular characters of leaves and leaf-like structures on vegetative and fertile organs of *Emporia cryptica* sp. nov.

Species/ Characters	Shape (face view)	Shape (side view)	Length (mm)	Width (mm)	Stomata				Papillae		Trichome bases (adx / abx)
					Structure	Distribution (adaxial / abaxial)	Number of stomata per band	Subsidiary cell number	Subsidiary cells	Epidermal cells	
Leaves on penultimate shoots	Nt, Li	Ss, Sp	2.4 - 7.1	0.6 - 2.0	Monocyclic, dicyclic	Two long, broad bands / two, three narrow bands	2 - 5	5 - 6	Overarching	Abundant	Few / abundant
Leaves on ultimate shoots	Nt, Li	Sss, Sc, Sp	1.2 -2.7	0.3 - 1.2	Monocyclic, dicyclic	Two long, broad bands / two, three narrow bands	2 - 12	5 - 8	Overarching	Abundant	Abundant / abundant
Leaves on branches with attached to pollen cones	Nt, Li	Sc, Sss	2.5 - 3.0	0.2 - 0.8	Monocyclic, dicyclic	Two long, broad bands / two narrow bands	2 - 11	7 - 8	Overarching	Abundant	Abundant / abundant
Microsporophylls	Tr	Sc	1.4 - 4.7	0.8 - 2.9	Monocyclic, dicyclic	Two long, broad bands / few scattered or none	2 - 8	5 -7	Overarching	Abundant	Abundant / abundant
Leaves on branches with attached to ovulate cones	Nt, Li	Ss, Sp	3 - 7	0.6 - 2.0	Monocyclic, dicyclic	Two long, broad bands / two narrow bands	2 - 5	5 - 6	Overarching	Abundant	Abundant / abundant
Bracts of ovulate cones	Nt, Li, Fr	Ss, Sc	5 - 8	2 - 3	Monocyclic, dicyclic	Two long, broad bands / two narrow bands	2 - 5	6 - 8	Overarching	Abundant	Abundant / abundant
Sterile scales of ovulate cones	Tr, l, Wo	Ss, Sp	1.5 - 3.2	0.7 - 1.2	Monocyclic, dicyclic	Two long, broad bands / two-three narrow bands	1 - 2	7 - 8	Overarching	Abundant	Abundant / abundant

Leaf shape abbreviations: El = Elliptical, Fr = Forked Tip, Li = Linear, l = Lanceolate, Ns= Narrow sub-triangular, Nt = Narrowly triangular, Ob= Oblong, Ov= Ovate, Wo = Widely oblong, Sc = Slightly concave, Sp= Spreading (extending nearly to the horizontal), Sq= Squamose (=scale like), Ss = S-shaped, Sss = Slightly S-shaped, St= Sub-triangular, Tr= Triangular._

Table 2. Comparison of morphological and cuticular characters of *Emporia cryptica* sp. nov. and ovulate cones of other Paleozoic conifers and coniferophytes. Characters that differ from those of *E. cryptica* are recorded in bold face type.

Organs/ Characters	Lateral branches	Penultimate leaves	Ultimate leaves	*Hetero phylly	Stomatal distribution (vegetative leaves)	Stomatal pattern Adx / Abx	Compound ovulate organ	Bract and ovuliferous dwarf shoot	Sporophyll position / number	Pollen Cone	Microsporophylls	Pollen Sacs
Emporia cryptica	Plagiotropic	Simple	Simple	Absent	Amphistomatic	Two bands / two narrow bands	Cone	Fused at base	Interspersed with SS, 2	Simple	Simple	Adaxial
Emporia lockardii	Plagiotropic	**Simple and forked**	Simple	**Age and position dependent**	Amphistomatic	**Two bands / two short, narrow, ind. rows**	Cone	**Separate throughout**	Interspersed with SS, 1-3	Simple	Simple	Adaxial
Hanskerpia hamiltonensis	Plagiotropic	**Forked**	Simple	**Position dependent**	Amphistomatic	**Parallel rows / parallel rows**	**Cone/zone?**	Fused at base	Interspersed with SS, 1-2	?	?	?
Thucydia mahoningensis	Plagiotropic	Simple	Simple	Absent	**Adaxial**	Two bands / **absent**	**Fertile zone**	**Separate throughout**	**Terminal, 3-4**	**Compound**	Simple	**Terminal**
Utrechtia floriniformis	Plagiotropic	**Forked**	Simple	**Position dependent**	Amphistomatic	Two bands / two bands	Cone	**Separate throughout**	**Terminal, 1**	Simple	Simple	Adaxial
Otovicia hypnoides	Plagiotropic	**Forked**	Simple	**Position dependent**	**Primarily adaxial**	Two bands / **scattered**	Cone	**Separate throughout**	Interspersed with SS, 2	Simple	Simple	Adaxial
Ernestiodendron filiciforme	Plagiotropic	Simple	Simple	Absent	Amphistomatic	**Parallel rows / parallel rows**	Cone	**Separate throughout**	**Terminal. 1**	Simple	Simple	?
Barthelia furcata	**Irregular**	**Forked**	**Simple & forked**	**Size dependent**	**Adaxial**	Two bands / **absent**	**Fertile zone**	**Separate throughout**	Interspersed with SS, ?	Simple	**Forked**	Adaxial

Modified from Rothwell et al., 2005. * Heterophylly is based on differences in the shape of leaves, where two distinctive types of leaves are known. Adx = adaxial surface, Abx =abaxial surface, SS = sterile scales.

Table 3. Comparison of leaves using morphological characters of *Emporia cryptica* sp. nov. Characters that differ from those of *E. cryptica* are recorded in bold face and overlapping characters are recorded in italics.

Species/ Characters	Stem	Lateral branches	Penultimate leaves				Ultimate leaves						*Heterophylly
			Length (mm)	Width (mm)	Shape (face view)	Shape (side view)	Length (mm)	Width (mm)	Shape (face view)	Shape, (side view)	Angle of Divergence Base	Apex	
Emporia cryptica	Orthotropic	Plagiotropic	2.4-7.1	0.6-2.0	Nt, Li	Ss, Sp	1.2-2.7	0.3-1.2	Nt, Li	Sss, Sc, Sp	30-64	27-70	Present
[1] *Emporia lockardii*	Orthotropic?	Plagiotropic	*5-10*	*1.0-2.1*	*Nt, Li*, Fr	Sc, Sss	1.7- 5.0	*0.4-1.16*	Nt, Li	*Sc, Sss*	*26-63*	28-69	Present
[2] *Hanskerpia hamiltonensis*	Orthotropic?	Plagiotropic	13-29	*1.0-1.74*	*Li*, Fr	*Sp*	5-15	*0.6-1.1*	*Li*	*Sc, Sp*	*30-45*	*32-50*	Present
[3] *Thucydia mahoningensis*	Orthotropic	Plagiotropic	*5.0-12.5*	*1.0-1.5*	Nt, Li	Sc, *Ss*	3-6	*0.4-1.0*	Nt, Li	[a] *Sc, Ss*	*22-57*	*21-54*	Absent
[4] *Utrechtia floriniformis*	Orthotropic?	Plagiotropic	12.0-25.0	*1.5-3.0*	*Nt, Li*, Fr	Sc	9-13	*0.4-0.6*	Nt, Li	*Sc, Ss*	?	*30*	Present
[5*] *Lebuchia garnettensis*	?	Plagiotropic	*3.0-16.0*	*1.5-2.5*	Nt, Li	Sc	4-7	*0.4-1.4*	Nt, Li	*Sc, Ss*	*35-70*	?	Absent
[6] *Otovicia hypnoides*	?	Plagiotropic	*2.0-8.0*	*1.0-1.5*	St, La, Fr	[a] Fa, *Ss*	1.5-4.0	0.2-0.5	Nt, Li	[a] Fa	*35-90*	*35*	Present
[2] *Ernestiodendron filiciforme*	?	Plagiotropic	10.0-23.0	*1.5-3.5*	Nt, Li	[b]Sc, *Sp*	7-15	1.5-2.0	Nt, Li	*Sp*	70-110	15	Absent
[7] *Barthelia furcata*	?	Irregular	22-47	<4.0	*Li*, Fr	Li, Sc	10-25	Up to 4.0	*Li*	Li, *Sc*	25-35	*14-25*	Present

Modified from Hernandez-Castillo et al., 2001b. [1] Hernandez-Castillo et al 2005a, including measurements of Mapes and Rothwell, 1984, 1991. [2] Florin 1938-45. [3] Hernandez-Castillo et al 2001 b. [4] Mapes and Rothwell 1991. [5*] Emended by Winston (1984). [6] Kerp et al. 1990; however, leaf measurements were taken from Florin (1938-45) because such data are not available in Kerp et al. 1990. [7] Rothwell and Mapes 2001.

Leaf shape abbreviations: El = Elliptical, Fr = Forked Tip, Li = Linear, Ns= Narrow sub-triangular, Nt = Narrowly triangular, Ob= Oblong, Ov= Ovate, Sc = Slightly concave, Sl= Slightly lanceolate, Sp= Spreading (extending nearly to the horizontal), Sq= Squamose (=scale like), Ss = S-shaped, Sss = Slightly S-shaped, St= Sub-triangular, Tr= Triangular.
* Heterophylly is based on differences in the shape of leaves, where two distinctive types of leaves are known. a, b, and c refer to leaf shape according to table 2 of Hernandez-Castillo et al 2001b.

Table 4. Comparison of cuticular features of leaves on ultimate shoots of *Emporia cryptica* sp. nov. and other Paleozoic conifers. Characters that differ from those of *E. cryptica* are recorded in bold face and overlapping characters are recorded in italics.

Species/ Characters	Stomatal distribution adaxial	Stomatal distribution abaxial	Stomatal complex structure	Stomatal complex size (µm)	Subsidiary cell number	Subsidiary cell papillae	Marginal trichomes	Trichome bases adaxial	Trichome bases abaxial	Epidermal papillae adaxial	Epidermal papillae abaxial
Emporia cryptica	Two long bands	Two narrow bands	Monocyclic and dicyclic	53 x 44	5 - 8	Present	Present, short and long	Present, abundant	Present, abundant	Present	Present
[1] *Emporia lockardii*	Two long bands	*Two short, narrow,* **ind. rows**	*Monocyclic*	58 x 46	*5 - 9*	Present	Present, short and long	**Few or absent**	Present abundant	Present	Present
[2] *Hanskerpia hamiltonensis*	**Parallel rows**	**Parallel rows**	*Monocyclic*	30 x 70	*5 - 6*	Present	*Present, short*	*Present*	Present abundant	Present	Present
[3] *Thucydia mahoningensis*	Two long bands	**Absent**	*Monocyclic*	24 x 20	*6 - 8*	Present	*Present*, **large**, *short*, **hair-like**	**Absent**	Present, abundant	Present	**Absent**
[4] *Utrechtia floriniformis*	Two long bands	**Two short bands, variable**	*Monocyclic*	50 x 55	*5 - 9*	Present	***Present, short,*** **hair-like**	*Present*	Present, abundant	Present	Present
[5] *Lebachia garnettensis*	Two long bands	**Few, scattered**	*Monocyclic*	[8]45 x 40	**More than 10?**	**Absent**	*Present, short,* **hair-like**	**Absent**	Present abundant	?	?
[6] *Otovicia hypnoides*	Two long bands	**Few stomata groups**	*Monocyclic,* **incompletely dicyclic**	70 x 60	5 - 8	Present	*Present*, **conical**	*Present*	Present abundant	Present	Present
[2] *Ernestiodendron filiciforme*	**Parallel rows**	**Parallel rows**	*Monocyclic,* **incompletely dicyclic**	[8]60 x 40	*4 - 8*	Present	*Present, short,* **hair-like**	*Present*	Present abundant	**Absent**	Present
[7] *Barthelia furcata*	Two long bands	**Absent**	**Monocyclic**	36 x 63	4 - 7	Present	**Present, short, hair-like**	Present	Present, abundant	Present	Present

Modified from Hernandez-Castillo et al., 2001b. [1] Hernandez-Castillo et al 2005a, including Mapes and Rothwell, 1984, 1991. [2] Florin 1938-45. [3] Hernandez-Castillo et al 2001 b. [4] Mapes and Rothwell 1991. [5*] Emended by Winston (1984). [6] Kerp et al 1990; however, leaf measurements were taken from Florin (1938-45) because such data are not available in Kerp et al 1990. [7] Rothwell and Mapes 2001. [8] Measured directly from Florin's monograph (1938-45).

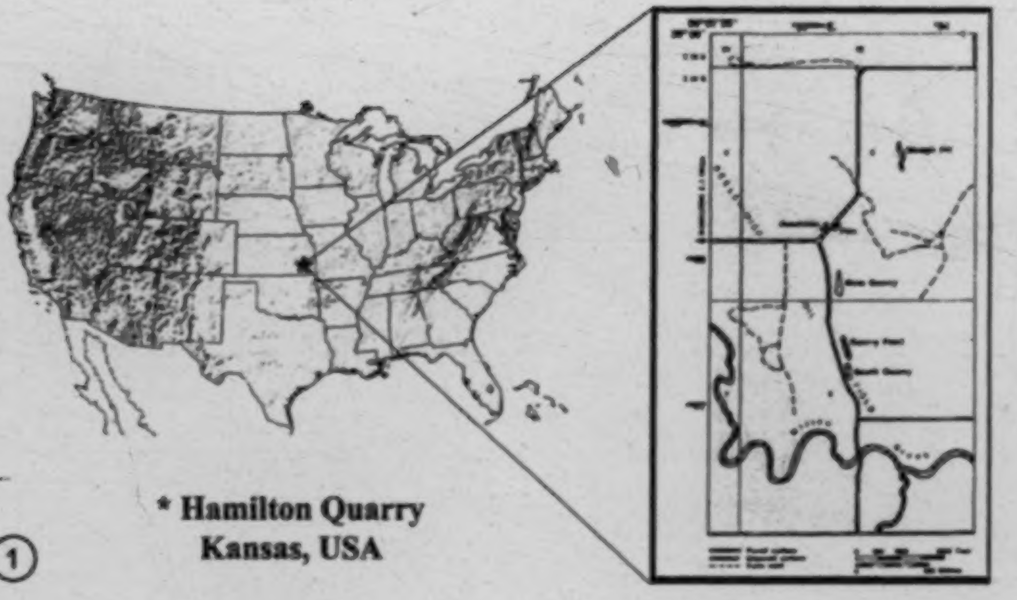
Table 5. Characters of compound ovulate cones and zones of *Emporia cryptica* sp. nov. and those of other Paleozoic conifers. Characters that differ from those of *E. cryptica* are recorded in bold face and overlapping characters are recorded in italics.

Species/ Characters	Ovulate fructification	Cone Morphology			Bract	Dwarf shoot				Ovules
		Length (cm)	Width (cm)	Shape		Symmetry	Number of sterile scales	Position of sporophylls	Number of sporophylls*	
Emporia cryptica	Terminal cone	5.0-6.2	0.7-1.2	Ellipsoidal	Forked	Bilateral	20-25	Interspersed with SS	2	Terminal, Inverted
[1] *Emporia lockardii*	Terminal cone	**2.8-5.0**	*1.1-1.5*	**Cylindrical to** ***ellipsoidal***	Forked	Bilateral	*14-30*	Interspersed with SS	*1 - 3*	Terminal, Inverted
[2] *Hanskerpia hamiltonensis*	**Terminal cone/zone?**	**11.0**	**2.7**	**Cylindrical**	Forked	Bilateral	**<15?**	Interspersed with SS	*1-2*	Terminal, Inverted
[3] *Thucydia mahoningensis*	**Fertile Zone**	**3.0-4.5**	*0.9-1.5*	**Cylindrical to** ***ellipsoidal***	**Simple**	Bilateral	**10-15**	**Terminal**	**3 - 4**	Terminal, Inverted
[4] *Utrechtia floriniformis*	Terminal cone	**7.0**	*1.2*	**Cylindrical to** ***ellipsoidal***	Forked	Bilateral	**>10**	**Terminal**	**1**	Terminal, Inverted
[5] *Lebachia garnettensis*	Terminal cone	**2.0-3.0**	**0.10-0.15**	Ellipsoidal	Forked	Bilateral	**<5?**	**?**	**[*]≥3?**	**?**
[6] *Otovicia hypnoides*	Terminal cone	*3.0-6.5*	**1.1-1.8**	**Cylindrical**	Forked	Bilateral	**>10**	Interspersed with SS	2	Terminal, Inverted
[2] *Ernestiodendron filiciforme*	Terminal cone	**10.0-20.0**	**2.2-3.0**	Ellipsoidal	Forked	Bilateral	**5-10**	**Terminal?**	**1**	Terminal, Inverted
[7] *Barthelia furcata*	**Fertile zone**	**Up to 16**	**2.4-2.6**	**Cylindrical to** ***ellipsoidal***	Forked	**Radial**	**?**	**Terminal**	**?**	Terminal, Inverted?

Modified from Hernandez-Castillo et al., 2001b. [1] Hernandez-Castillo et al 2005a, including Mapes and Rothwell, 1984, 1991. [2] Florin 1938-45. [3] Hernandez-Castillo et al 2001 b. [4] Mapes and Rothwell 1991. [5*] Emended by Winston (1984). [6] Kerp et al 1990; however, leaf measurements were taken from Florin (1938-45) because such data are not available in Kerp et al 1990. [7] Rothwell and Mapes 2001. * Fertile scale as in Florin, Clement-Westerhof (1984) and Kerp et al. (1990) concepts. SS= sterile scales.

Figure Captions

Fig. 1. Map of the USA showing location of the Hamilton Quarry locality, Kansas.


* Hamilton Quarry
Kansas, USA

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Figs. 2-3. *Emporia cryptica* sp. nov., branches. 2. Antepenultimate shoot (arrowhead) with penultimate shoots (p) and ultimate shoots with helically arranged leaves (bracket). M 2789 B. 3. Counterpart of Fig. 2 showing five penultimate shoots (p) with attached ultimate shoots bearing concave to slightly concave leaves (bracket). M 2789 B, scale bars = 2 cm.

P
2

P
3

Figs. 4-7. *Emporia cryptica* sp. nov., lateral branches. **4.** Branch showing deltoid shape; penultimate shoot with leaves (arrowhead), and ultimate shoots with linear to concave leaves. M 3004 C, scale bar = 2 cm. **5.** Penultimate shoot with leaves (arrowheads) and ultimate leafy shoots. M 4013, scale bar = 1 cm. **6.** Irregular branching of ultimate shoots. M 233, scale bar = 1 cm. **7.** Branch showing deltoid shape of leaves on penultimate shoots (arrowheads) and slightly concave shape of leaves on ultimate shoots. M 760, scale bar = 1 cm.

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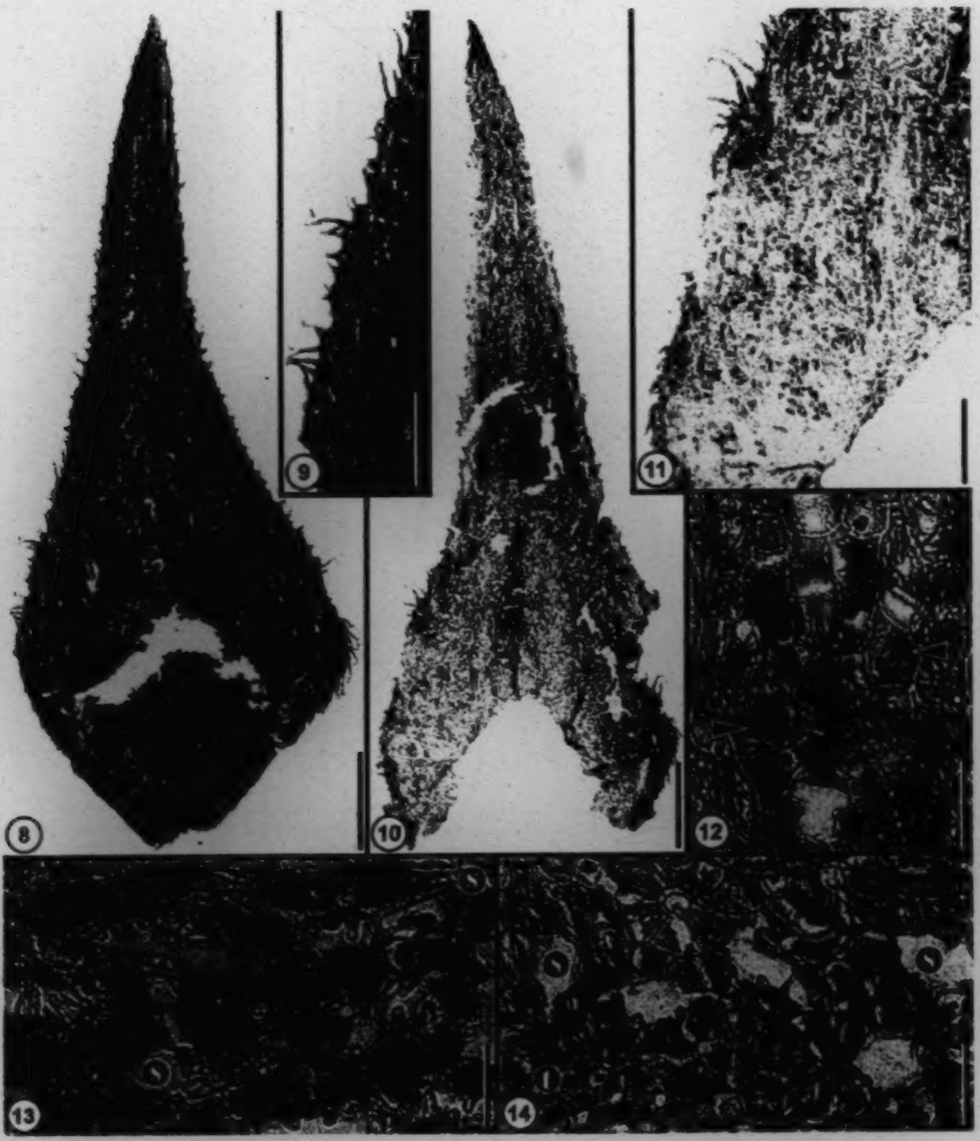
Figs. 8-14. *Emporia cryptica* sp. nov., cuticular macerations of leaves on penultimate shoots. Specimens macerated from M 2970. All images from adaxial surfaces unless otherwise indicated. **8.** Leaf showing narrowly triangular shape with broad base and marginal trichomes. Scale bar = 800 µm. **9.** Marginal trichomes of Fig. 8. Scale bar = 200 µm. **10.** Leaf showing marginal trichomes and numerous dicyclic stomata (dark dots) throughout the leaf. Scale bar = 600 µm. **11.** Marginal trichomes. Scale bar = 200 µm. **12.** Dicyclic stomata with papillate outer subsidiary cells (arrowheads). Scale bar = 15 µm. **13.** Stomata (s) showing five subsidiary cells with large overarching papillae. Scale bar = 15 µm. **14.** Abaxial narrow band of stomata (s) showing subsidiary cells with overarching papillae, and trichome bases (t). Scale bar = 15 µm.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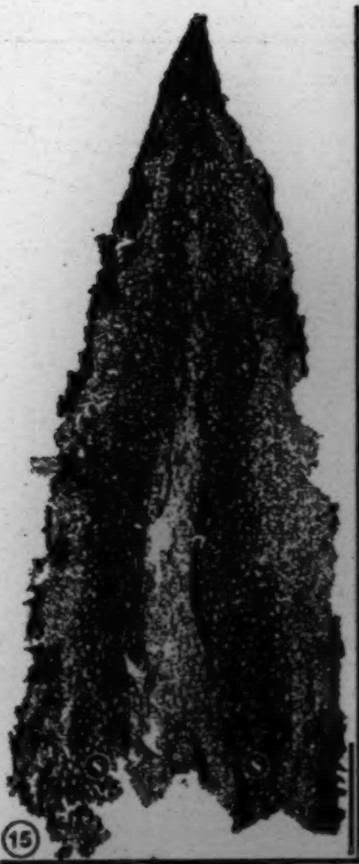
Figs. 15-21. *Emporia cryptica* sp. nov., cuticular macerations of leaves on ultimate shoots. Specimens macerated from M 1279. **15**. Adaxial surface showing subtriangular shape, and two broad bands of stomata (s) separated by stomatal free zone. Scale bar = 500 μm. **16**. Adaxial surface with marginal trichomes (at left), papillate epidermal cells, trichome bases (t), and stomatal band (s). Scale bar = 800 μm. **17**. Adaxial surface showing dicyclic stomata (dark areas). Scale = 800 μm. **18**. Dicyclic stomata (bracket). Scale bar = 25 μm. **19**. Adaxial stomata showing six subsidiary cells with broad overarching papillae. Scale bar = 300 μm. **20**. Abaxial surface narrow stomatal bands (s). Scale bar = 500 μm. **21**. Abaxial trichome bases (t) and narrow stomatal band with two stomatal complexes (s). Scale bar = 25 μm.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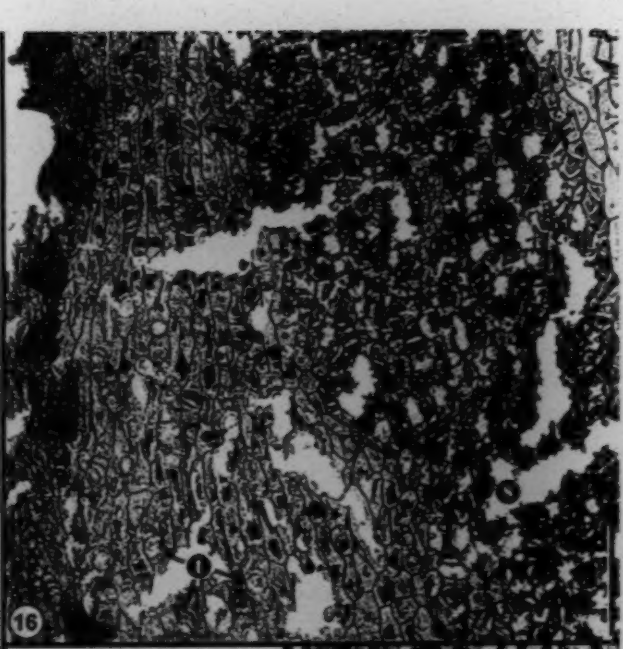
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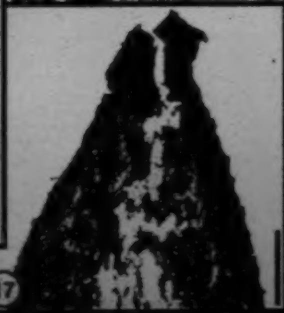
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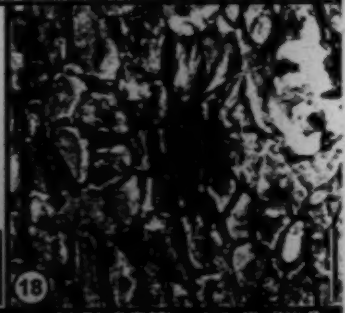
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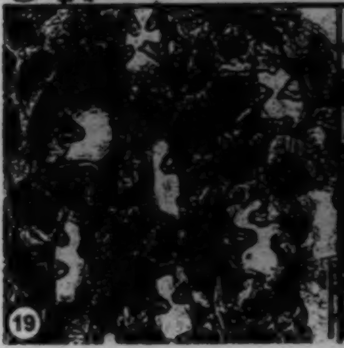
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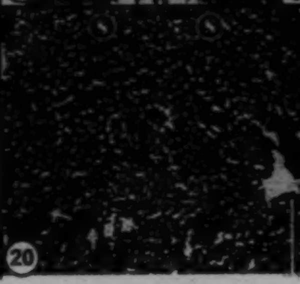
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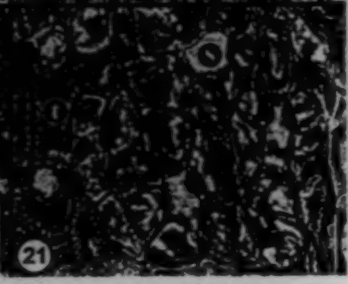
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Figs. 22-25. *Emporia cryptica* sp. nov., pollen cones. **22**. Mature ellipsoidal cone attached to ultimate shoot. Note triangular microsporophylls, and slightly-concave leaves on ultimate shoots. M 1061, scale bar = 5 mm. **23.** Detached ellipsoidal mature cone. M 2904 A, scale = 5 mm. **24**. Immature cone with attached ultimate shoot. M 1055, scale bar = 5 mm. **25**. Broken cone showing central cone axis and departing peltate microsporophylls. M 3010, scale bar = 5 mm.

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Figs. 26-27. *Emporia cryptica* sp. nov., leaves on ultimate shoot with attached pollen cone. **26**. Adaxial surface showing subtriangular shape, two bands of stomata (s) and dicyclic stomata (dark dots). M 170-2, scale bar = 800 μm. **27**. Adaxial surface showing trichome bases (t), papillate epidermal cells, and stomata (s) with subsidiary cells and overarching papillae. M 1823-6, scale bar = 500 μm.

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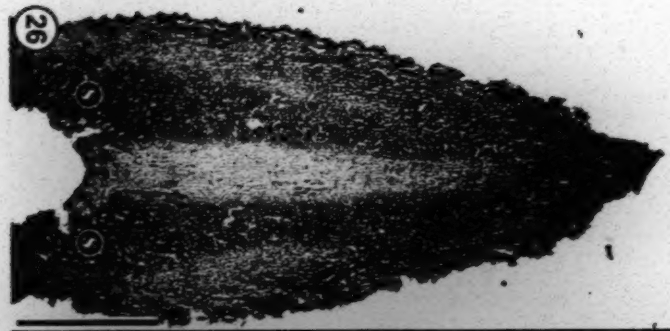

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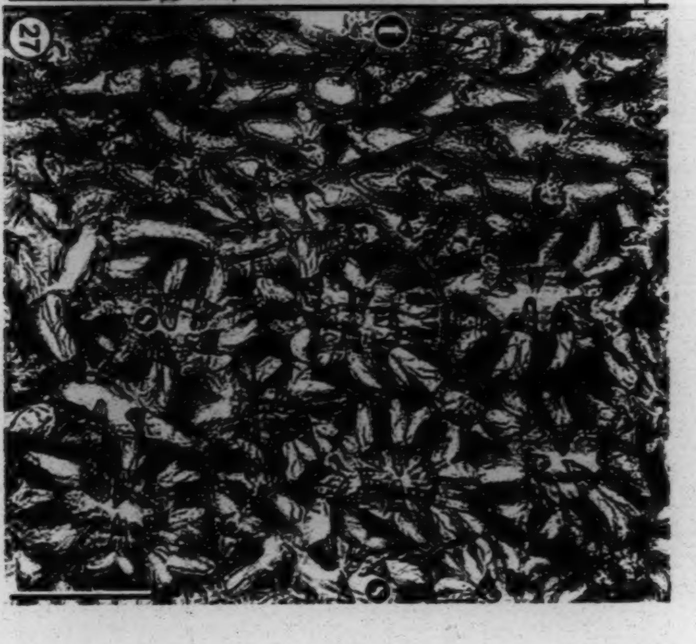

Figs. 28-33. *Emporia cryptica* sp. nov., SEM microsporophylls. Specimens macerated from M 1625. **28**. Microsporophyll showing adaxial surface with triangular shape, stomatal bands (s) and marginal trichomes. Scale bar = 500 µm. **29**. Sporophyll showing adaxial trichome bases, papillae, and marginal trichomes. Scale bar = 50 µm. **30**. Adaxial stomatal bands (s) and stomatal free zone (center). Scale bar = 100 µm. **31**. Stomatal complex showing five subsidiary cells with erect to slightly overarching papillae. Scale bar = 10 µm. **32**. Microsporophyll showing abaxial surface and marginal uniseriate trichomes. Scale bar = 500 µm. **33**. Abaxial trichome bases showing circular to ellipsoidal shape. Scale bar = 40 µm.

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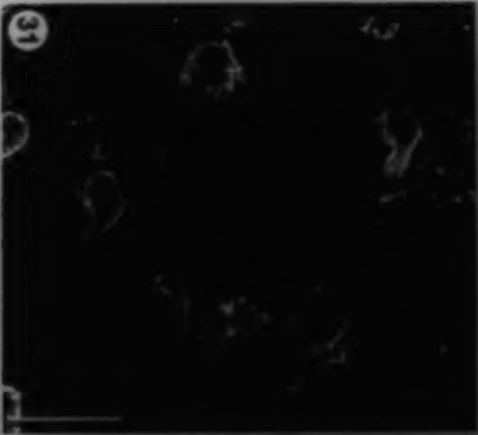
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Figs. 34-40. *Emporia cryptica* sp. nov., pollen cone radial sections and in situ *Potonieisporites* prepollen grains. **34**. Section of immature cone attached to ultimate leafy shoot. M 170-5, scale bar = 2 mm. **35**. Microsporophylls with adaxial pollen sacs (arrowhead). M 170-11, scale bar = 500 μm. **36**. Stalk showing attached pollen sacs (arrowheads). M 170-5, scale bar = 500 μm. **37**. Microsporophylls showing distal lamina with upturned tip (bracket), and adaxial pollen sacs (arrowheads). M 170-11, scale bar = 340 μm. **38**. Pollen sac (bracket) showing *in situ* monosaccate prepollen grains. M 170-5, scale bar = 120 μm. **39**. Distal view of grain. M 170-11, scale bar = 20 μm. **40**. Distal view of grain showing saccus, central body and parallel folds. M 170-11, scale bar = 25 μm.

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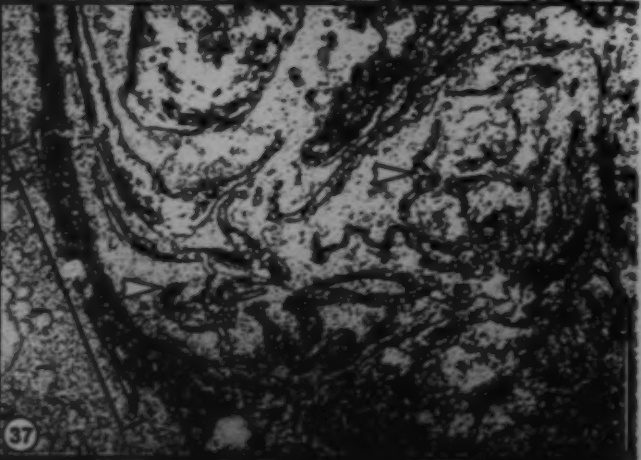
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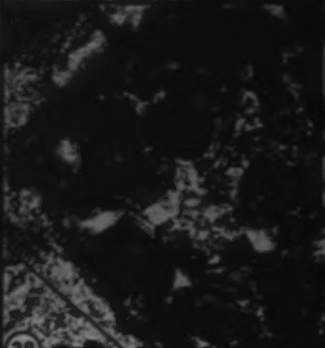
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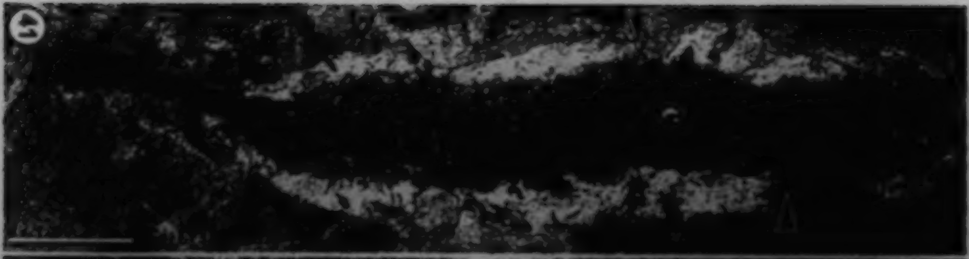
Figs. 41-43. *Emporia cryptica* sp. nov., ovulate cones. **41**. Mature narrow, elliptical cone with attached penultimate shoot. Note cone axis (c) with bracts (arrowheads) subtending axillary dwarf shoots. M 1642 A, scale bar = 1.5 cm. **42**. Cone showing attached penultimate shoot with leaves at base (arrowhead). M 1399, scale bar = 1 cm. **43**. Cone base showing leaf on penultimate shoot (white arrowhead), cone axis (c), and subtending bract (black arrowhead) with axillary dwarf shoot. M 1602, scale bar = 1 cm.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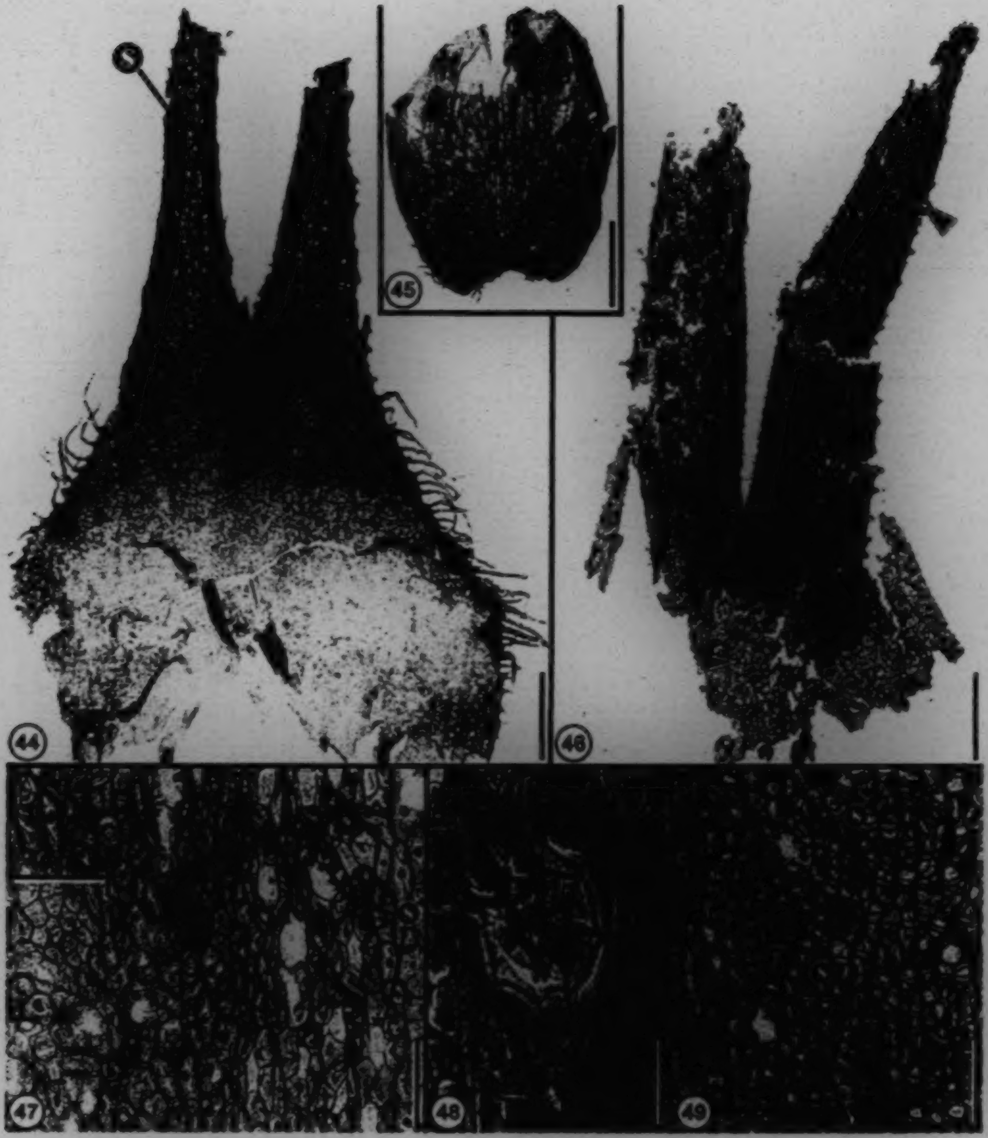
Figs. 44-49. *Emporia cryptica* sp. nov., bracts from ovulate cones. **44.** Adaxial surface showing forked tip, broad base and bands of stomata (s) on forked tips. M 2983-7, scale bar = 1.5 mm. **45.** Adaxial surface of bract base showing surface trichomes. M 1613-9, scale bar = 1.2 mm. **46.** Forked tip showing adaxial dicyclic stomata (arrowheads). M 1613-8, scale bar = 500 μm. **47.** Adaxial dicyclic stomata (bracket) and narrow band of stomata (s). M 1613-Br1, scale bar = 180 μm. **48.** Adaxial non-functional dicyclic stoma and papillate epidermal cells. M 1613-Br1, scale bar = 80 μm. **49.** Abaxial papillate epidermal cells (left), scattered stomata (s) and trichome bases (right). M 1613-8, scale bar = 150 μm.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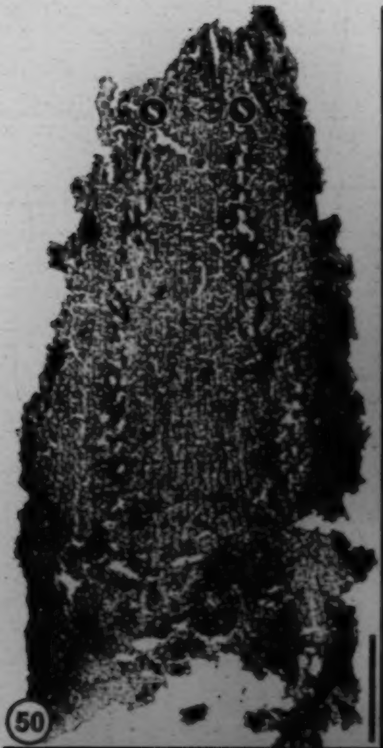
Figs. 50-53. *Emporia cryptica* sp. nov., ovulate cone sterile scales. **50.** Adaxial surface showing two narrow bands of stomata (s). M 2970-10, scale bar = 400 μm. **51.** Abaxial surface showing three narrow bands of stomata (s). M 2970-11, scale bar = 400 μm. **52.** Adaxial stomata (s) showing subsidiary cells and overarching papillae. M 2970-10, scale bar = 50 μm. **53.** Abaxial stomata (s) showing subsidiary cells with overarching papillae and trichome bases (left). M 2970-11, scale bar = 40 μm.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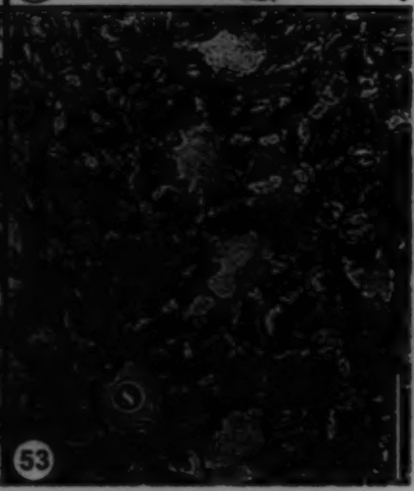
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Figs. 54-57. *Emporia cryptica* sp. nov., SEM of sterile scales, sporophylls, and seed. Specimens macerated from M 2978 A. **54.** Lanceolate scale with marginal trichomes. Scale bar = 500 μm. **55.** Widely obovate scale with marginal trichomes. Scale bar = 250 μm. **56.** Adaxial surface showing sporophyll and sub-apical seed scar. Scale bar = 250 μm. **57.** Seed showing trichome bases (top left). Scale bar = 500 μm.

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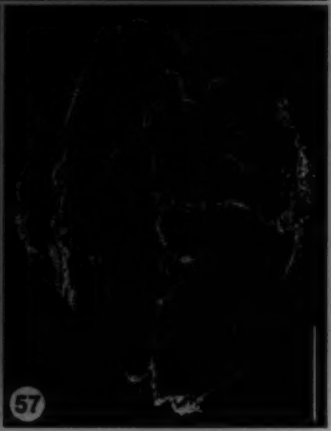
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Figs. 58-62. *Emporia cryptica* sp. nov., stem anatomy. **58.** Longitudinal section of cone axis showing secondary xylem (2x), primary xylem (1x) flanking pith with parenchyma cells and secretory cells (arrowheads). M 1613- MP17, scale bar = 200 μm. **59.** Longitudinal section showing elongate secretory cells (arrowheads). M 1613- MP17, scale bar = 200 μm. **60**. Longitudinal section showing spiral thickenings of primary xylem tracheids. M 1613- MP17, scale bar = 200 μm. **61.** Radial section of secondary xylem showing groups of polygonal circular bordered pits on radial walls of tracheids. M 1613- MP17, scale bar = 200 μm. **62.** Tangential section showing uniseriate rays one to two cells high. M 1613- MP17, scale bar = 200 μm.

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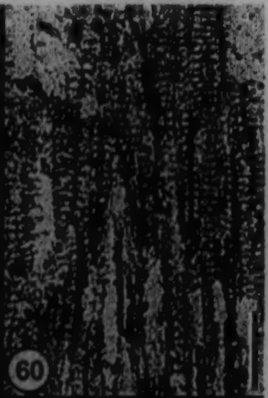

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Figs. 63-69. *Emporia cryptica* sp. nov., ovulate cone anatomy. **63**. Longitudinal section showing cone axis (C), bract (B), and axillary dwarf shoots with sterile scales (Ss) and seeds (Se). Note seed micropyles at arrowheads. M 1613- MP24, scale bar = 1 mm. **64**. Longitudinal section showing bracts (B) subtending axillary dwarf shoots with sterile scales (Ss) and seeds (Se). Holotype M 1613, scale bar = 0.6 mm. **65**. Cross section of axillary dwarf shoot showing sterile scales (Ss) and two seeds. M 2984 B-17, scale bar = 300 μm. **66**. Winged seed showing integuments (In) and nucellus (N). M 2983 B- MP17, scale bar = 200 μm. **67**. Transverse section of seed at micropylar end showing integuments (In) and nucellar beak (Nb). M 2983 B- MP17, scale bar = 150 μm. **68**. Nucellar beak (Nb) with enclosed prepollen grain. M 2983 B-17, scale bar = 45 μm. **69**. Monosaccate prepollen grain of Fig. 68. M 2983 B-17, scale bar = 30 μm.

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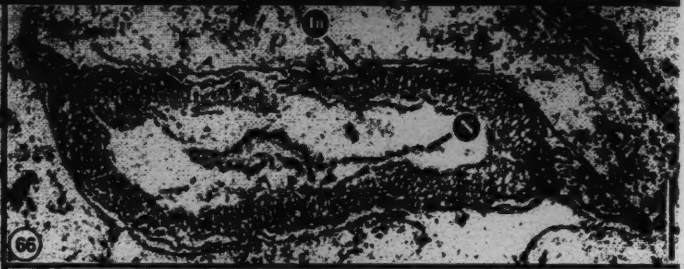

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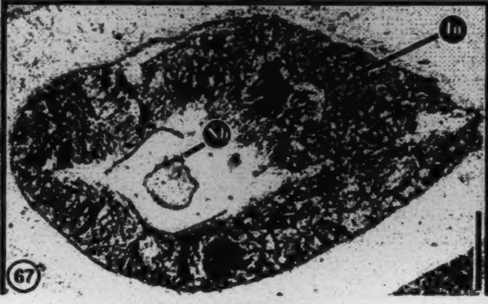

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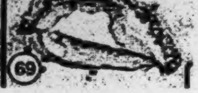

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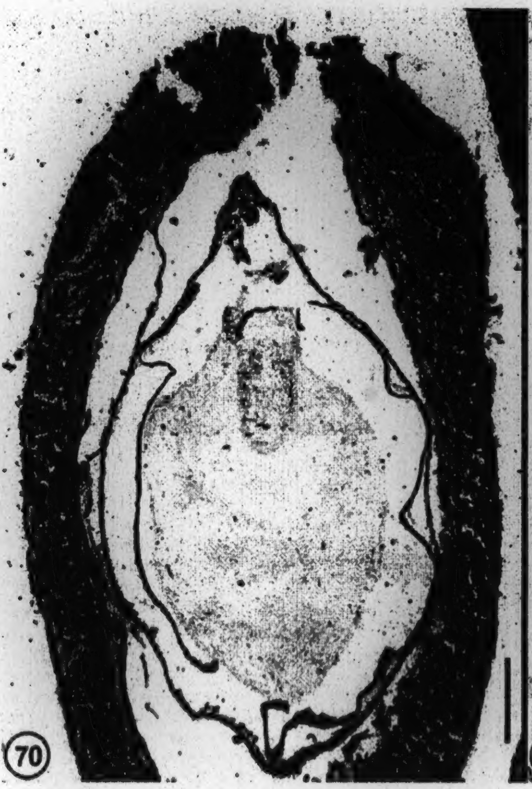
Figs. 70-72. *Emporia cryptica* sp. nov., anatomy of ovule and seeds. **70.** Longitudinal section of ovule showing integuments (In), nucellus with two pollen grains and open micropylar end (Mi). M 1613-MP21, scale bar = 400 μm. **71.** Seed showing integuments (In), micropyle (mi), and embryo remains (e). M 1613- MP30, scale bar = 800 μm. **72.** Seed showing integuments (arrowhead), micropyle (mi), megaspore membrane (mm), cellular megagametophyte (m), and embryo (e). M 1613- MP34, scale bar = 800 μm.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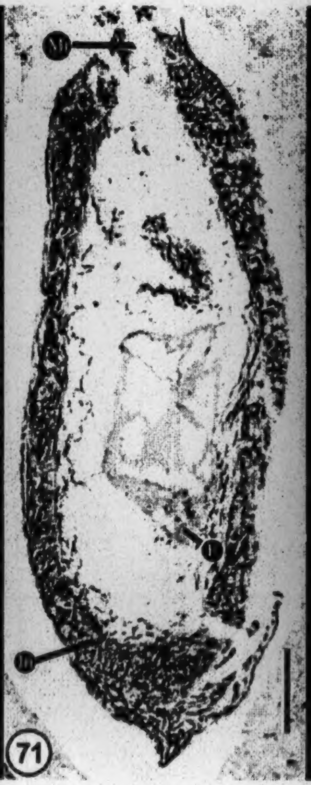
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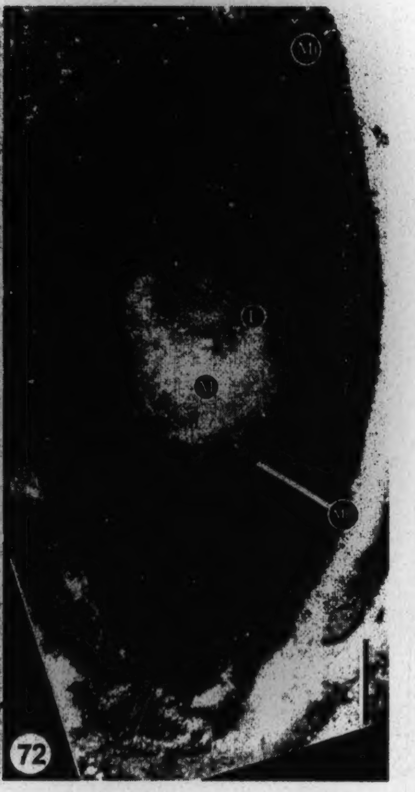
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CHAPTER 5

A new fossil conifer (*Emporia royalii* sp. nov.: Emporiaceae) from the Hamilton Quarry (upper Pennsylvanian), Kansas, USA.

Introduction

The Late Pennsylvanian Hamilton Quarry yields an exceptionally well preserved and rich fauna and an abundant terrestrial flora (Mapes and Mapes 1988; Rothwell and Mapes 1988, 2001; Fahrer et al. 1990; Fahrer 1991; Feldman et al. 1993). Floristic analyses have shown a conifer dominated flora derived from relatively dry basinal slopes (DiMichelle and Aronson 1992; Rothwell et al. 1997). Previous studies of the Hamilton Quarry flora include the first and most complete description of internal anatomy of Paleozoic conifers, and the first evidence of inverted ovules (Mapes and Rothwell 1984), the origin of conifer seed dormancy (Mapes et al. 1989), and the first description of simple pollen cones with adaxial pollen sacs (Mapes and Rothwell 1998). These well-preserved fossil plants have allowed the reconstruction of three species of the family Emporiaceae (Mapes and Rothwell 1991, 2003; Rothwell et al. 2005; chapters 3-4 in this dissertation).

The fossil record of the most ancient conifers can be traced back to the Upper Carboniferous (Pennsylvanian and early Permian) of Europe and North America (Florin 1938-45; Galtier et al. 1992; Rothwell, 1982; Rothwell et al. 1997). These euramerican conifers, also referred to as “walchian” conifers (Mapes and Rothwell 1984), are classified in several families within the order Voltziales (Florin 1938-45; Visscher et al. 1986; Kerp et al. 1990; Mapes and Rothwell 1991). The first and most significant systematic work for these plants was proposed by Rudolph Florin (1927, 1938-45, 1950, 1951). His work stood more or less unchallenged until recent studies called to question Florin’s systematics and interpretations of the most primitive conifers (Schweitzer 1963, 1996; Rothwell 1982; Clement-Westerhof 1984, 1987, 1988; Mapes and Rothwell 1984, 1991, 1998; Meyen 1984; Winston 1984; Visscher, et al. 1986; Kerp, et al. 1990; Kerp and Clement-Westerhof

1991; Hernandez-Castillo et al., 2001a).

A summary and a complete reevaluation and reexamination of these ancient conifers has been previously presented (Hernandez-Castillo et al., 2001a) and lead to the creation of new reliable methodologies and criteria for circumscribing species of walchian conifer plants based on the correlation of numerous vegetative branches to both pollen and ovulate cones. This correlation among individual plant organs relies on similarities among morphological, cuticular and anatomical characters of vegetative and fertile organs (Hernandez-Castillo et al. 2001b). In the current study, I employ this approach to describe *Emporia royalii* sp. nov.

Emporia royalii is the fifth conifer reconstructed from the Hamilton Quarry (Rothwell and Mapes 2001; Rothwell et al. 2005; chapters 3-4 in this dissertation). Four out of five of these completely reconstructed conifers belong to the family Emporiaceae (Mapes and Rothwell 1991, 2003; chapters 3-4 in this dissertation) making it the best known family of walchian conifers from the Paleozoic worldwide. The Hamilton Quarry is the only locality in the world where all conifers have been described as complete plants. The reconstruction provided here is part of broader study to reinvestigate, describe, and reevaluate morphological characters, and reconstruct species of euramerican Paleozoic walchian conifers, so they can be used to resolve systematic relationships among the conifers as a whole.

Materials and Methods

The specimens used in this study are preserved as coalified compressions with preserved cuticles and cellular permineralization. They occur in Late Pennsylvanian laminated carbonate mudstones of the Hartford Limestone, Topeka Limestone Formation, Shawnee Group, located east of Hamilton, Kansas, USA (Fig. 1; Mapes and Rothwell 1984; Bridge 1988; French et al. 1988; Busch et al. 1988). These beds represent channel deposits in an estuarian environment under tidal influence (French et al. 1988; Fahrer et al. 1990; Fahrer 1991; Feldman et al. 1993). *Emporia royalii sp. nov.* is represented by 109 specimens. Twenty eight of these are plagiotropic leafy branching systems with penultimate and ultimate shoots attached; four have cuticles preserved, and two are anatomically preserved. Seventy are pollen cones, 22 of which are attached to ultimate shoots. Eight have cuticles preserved and nine are anatomically preserved. Eleven are ovulate cones. Five of them are attached to penultimate shoots with leaves, three have cuticles; and three are anatomically preserved.

Specimens were initially revealed on split surfaces of the limestones. Cuticles were macerated from the matrix with dilute (0.5-1%) HCl, rinsed in distilled water, bleached in Lysol toilet bowl cleaner (Reckitt Benckiser, Toronto, Canada), allowed to air dry on microscope slides, and mounted under a cover slip with Eukitt (O. Kindler GmbH Co., Freiburg, Germany). Cuticles for scanning electron microscopy were air dried on specimen stubs and coated with (100 Å) gold, and examined on a JEOL (Japan Electron Optics Ltd.) 6301 FXV and a Phillips XL30 ESEM (FEI Co., Tokyo, Japan) scanning electron microscopes. Some anatomically preserved specimens were prepared with the cellulose acetate peel technique (Joy et al. 1956), and others were cut into wafers and ground thin enough to transmit light. Compressed specimens with some anatomical preservation were etched with 1-5% HCl, flooded with acetone, and a cellulose acetate peel was placed on the split surface. These surface pulls were removed while the acetate was still plastic enough to be pressed relatively flat under a heavy weight. Light microscopy was conducted using Zeiss Ultraphot IIIB and WL microscopes, and images captured with a MicroLumina digital scanning camera (Leaf Systems Inc., Bedford, MA) or a PhotoPhase digital scanning camera (Phase One A/S, Frederiksberg, Denmark). Images were processed using Adobe Photoshop. All specimens are housed in the Ohio University Paleobotanical Herbarium (OUPH), Athens, Ohio, USA.

Systematic Palaeontology

Order VOLTZIALES

Family EMPORIACEAE

Genus EMPORIA (Mapes and Rothwell) Mapes and Rothwell

Emporia royalii sp. nov. Hernandez-Castillo, Stockey, Rothwell & Mapes

Plates 1-15; Tables 1-5.

Holotype. Specimen M 2947 A (Fig. 11A); deposited at the Ohio University Paleobotanical Herbarium, Athens, OH.

Paratypes. Lateral branches M 1618, M 4021A, M 4018, M 4020, M 1626 A, M 2618. Cuticular features of leaves on penultimate shoots M 1627, M 1626, M 2986 B. Cuticular features of ultimate shoots M 1627, M 591. Pollen cones M 3985 B, M 1617, M 4004, M 591, M 2962, M 3099. Vegetative leaves of ultimate shoots attached to pollen cones M 591. Pollen cone macerations M 2962. Anatomically preserved pollen cones M 1631, M 80. Ovulate cones M 2947 A, M 1809, M 2969, M 1883, M1662. Ovulate cone macerations M 2986, M 1613, M 1883. Ovulate cone anatomy M 2986 B.

Type locality. Hamilton Quarry; NW quarter, sec. 5 and 8, T. 24 S., R.12E., Virgil seven and a half foot quadrangle, Greenwood County, Kansas, U.S.A. (Fig.1).

Lithology and Stratigraphy. Hartford Limestone, Topeka Limestone Formation, Shawnee Group.

Age. Late Pennsylvanian (Stephanian A).

Etymology. The specific epithet *royalii* honors Royal Mapes (Ohio University) for his enthusiastic collecting of fossils from this locality.

Specific diagnosis. Characters of species those of genus. Leaves on penultimate shoots simple to forked, narrowly triangular to linear (face view), slightly S-shaped to spreading (side view), 1.6-5.3 mm long, 0.3-1.5 mm wide. Leaves on ultimate shoots narrow, triangular to linear (face view), slightly S-shaped to slightly concave (side view), 1.6-4.5 mm long, 0.3-1.2 mm wide. Epidermal cells rectangular, elongate to polygonal, often unipapillate; marginal trichomes present, short. Adaxial stomatal bands, two, separated by elongate epidermal cells. Stomata monocyclic, 45 x 53 μm in diameter, 6-8 unipapillate subsidiary cells, guard cells sunken; undeveloped papillae in stomatal free zone present. Adaxial trichome bases few to none. Abaxial stomatal bands, two, narrow, or two single rows. Abaxial trichome bases abundant. Pith secretory cells present. Secondary xylem tracheids uniseriate-biseriate, bordered pits circular; wood rays 1-2 cells high. Outer cortex with axially aligned secretory cells. Pollen cones ellipsoidal to obovate, 0.5-3.2 cm long, 0.2-1.0 cm wide. Microsporophylls 0.25-4.1 mm long, 2.0-2.26 mm wide. Pollen sacs 6-10, adaxial, ellipsoidal, attached to a single area on shank. Microsporophyll distal lamina with 2-4 adaxial stomatal bands; stomata 45-58 μm long, 29-34 μm wide, 4-6 unipapillate subsidiary cells; epidermal cells unipapillate. Prepollen of *Potonieisporites* type, subcircular to circular in polar view, 107 μm long, 86 μm wide. Leaves on ultimate shoots subtending pollen cones like those on vegetative ultimate shoots. Ovulate cones ellipsoidal, 5.0-8.2 cm long, 1.1-1.6 cm wide. Bracts forked with cuticular features like those of forked leaves on penultimate shoots. Axillary ovuliferous dwarf shoots fused at base. Sterile scales triangular to lanceolate, apex mucronate, up to 45, 1.6-7.6 mm long, 0.5-2.0 mm wide, amphistomatic. Sporophylls narrow, 1-2 per dwarf shoot, covered by numerous trichome bases. Ovules bilateral, flattened, winged; base rounded to subcordate. Ovule attachment scar basal to sub-lateral; nucellus fused to integument except at micropyle; nucellar beak present; pollen chamber simple.

Description

Branching systems. The specimens consist of two orders of branching with a penultimate shoot that bears several ultimate shoots (Figs. 2A-2D). Branch shape ranges from ovoid to deltoid (Figs. 2A-2D, 3B). The largest plagiotropic branch measures 47 cm long and 9.6 cm wide (Fig. 2A). The longest ultimate shoots (ca. 8.6 cm long) occur in the mid-region of large branches (Fig. 2A). This shoot is plagiotropic, but the ultimate shoots are not located in the same plane, and they are all oriented toward the same side (Fig. 2A). All other branching specimens, however, are plagiotropic (Figs. 2B-2D, 3A, 3B). Most lateral branches are broken at the very base or the apex (Figs. 2A-2D, 3A, 3B). This indicates that some plagiotropic shoots were larger than the specimens under study. Penultimate shoots are 2.0 - 4.0 mm wide at the base of the preserved specimens (n = 14), and ultimate shoots are 1.0 - 2.4 mm wide at the base (n = 16).

Leaves on penultimate shoots. Leaves are helically arranged on penultimate and ultimate shoots (Figs. 2A-2D, 3A, 3B). Leaves are 1.6-5.3 mm long, and 0.3-1.5 mm wide, simple or forked (Table 1; Fig. 3C, 4A-4F, 5A). The simple leaves are often found on small and medium sized branches (Figs. 2A, 2B), while forked leaves are found on larger specimens (Figs. 1A-1D). Simple leaves are narrowly triangular with a broad base in face view and slightly S-shaped to S-shaped in side view (Figs. 3A-3C, 4A-4C). Forked leaves are a linear with a distal forking region tips that taper to a point (Figs. 2A, 2D). In side view, these forked leaves have a similar shape to simple leaves on the same shoot order.

Cuticular macerations reveal two adaxial bands of stomata, 2-6 stomata wide each having 5-6 subsidiary cells with overarching papillae (Table 1; Figs. 4A-4F). Stomata are monocyclic, ellipsoidal, and range 32-42 μm wide and 42-72 μm long (Figs. 4B). The length of some stomata may reach 85 μm long near the leaf base. Individual stomata may be in contact with adjacent stomata or separated by groups of epidermal cells (Fig. 4B). Bands of stomata are separated by a stomatal free zone of polygonal to rectangular epidermal cells (Figs. 4A) and elongate epidermal cells with what look like undeveloped papillae (Fig. 4D). In light microscopy, these structures appear as a "blurry line" in the center of the cell (Fig. 4D). Epidermal cells with small erect papillae are sometimes interspersed with surficial trichome bases particularly on the leaf margins (Figs. 4A-4C). The abaxial surface is completely covered by surficial trichome bases and has two rows of stomata, but these rows sometimes may be more one stoma wide forming a narrow stomatal band (Fig. 4C, 4E, 4F). Individual stomatal complexes have 6-8 subsidiary cells each with a single overarching papilla (Fig. 4F).

Leaves on ultimate shoots. Leaves are simple, helically arranged, 1.6-4.5 mm long and 0.3-1.2 mm wide. They are narrowly triangular to linear in face view (Figs. 3D, 5B) and slightly S-shaped to slightly concave in side view with numerous marginal trichomes (Figs. 2A-D, 3A, 3B, 3E, 3F). They diverge from stems at angles of 24-57° at base and 21-61° at the apex of the leaf. Leaves are amphistomatic with two adaxial bands of stomata (Figs. 3D, 3F, 5B) and two long bands of adaxial stomata (Figs. 5B, 5D). Stomatal bands are 4-8 stomata wide, separated by a stomatal free zone (Figs. 5B, 5D). Stomata are monocyclic, ellipsoidal to semicircular, 30-64 μm wide, and 41-84 μm long (average = 55 x 68 μm, n = 27), and have 6-8 subsidiary cells with erect or overarching papillae (Fig. 5D). Stomatal complexes may share subsidiary cells (Fig. 5D). Epidermal cells in marginal and stomatal free zones are elongate, rectangular, papillate, and are interspersed with undeveloped papillae. Trichome bases are not usually found among epidermal cells and marginal trichomes are often short or broken (Figs. 5B, 5D). The abaxial surface of leaves on ultimate shoots have numerous trichome bases and two single bands of stomata as in leaves from penultimate shoots (Fig. 4F).

Anatomy of stems. Stems have a parenchymatous pith with secretory cells surrounded by an endarch eustele with secondary xylem and leaf traces (Fig. 6A-6C). The pith is composed of polygonal parenchymatous cells and groups of secretory cells (Figs. 6D). Parenchyma cells are rectangular and elongate (Fig. 6D). Secretory cells with dark contents are located in the center of the stem and form horizontal plates in the pith (Fig. 6A, 6D). The primary xylem is composed of small diameter tracheids with annular or helical secondary wall thickenings (Fig. 6D, at arrow). Secondary xylem has rows of radially aligned tracheids that are hexagonal to circular in shape in cross section, separated by wood rays (Figs. 6A, 6C). In longitudinal section, tracheids show circular to hexagonal, uniseriate and occasionally biseriate bordered pits on the radial walls (Fig. 74). Wood rays are uniseriate, 1-2 cells high (Fig. 6F). The cortex contains rectangular parenchyma cells and secretory cells with dark contents (Fig. 6G). The epidermis is present on some specimens and shows a thick cuticle with numerous, often broken, trichomes (Fig. 6G).

Pollen cones. Pollen cones are simple, terminal, ellipsoidal to obovate, and 0.5-3.2 cm long, 0.2-1.0 cm wide (Figs. 7A-7F). Cones bear helically arranged microsporophylls, 0.25-4.1 mm long, 2.0-2.3 mm wide (Figs. 7A-7E). Microsporophylls have a narrowly triangular distal end and a broad base (Figs. 7C, 7E, 7F). These represent mature (Figs. 7B-C), intermediate (Figs. 7A, 7D-7E) and immature (Fig. 7F) pollen cones. Several pollen cones are often in organic connection with ultimate shoots that bear leaves (Figs. 7A, 7B, 7F), but many of them are isolated or broken (Figs. 7C-7E). Leaves on these attached shoots are simple and similar to those of penultimate shoots (Table 1). These leaves have two bands of stomata separated by a stomatal free zone, 2-6 stomata wide (Fig.

8A). Stomata are ellipsoidal with 6-8 papillate subsidiary cells and may share subsidiary cells (Fig. 8B). Leaf margins and stomatal free zones have rectangular epidermal cells, papillae, undeveloped papillae and lack trichome bases (Fig. 8B).

Cuticles of microsporophylls. Microsporophylls have 2-4 long, broad bands of adaxial stomata (Figs. 9A-9B). Two main bands run along the entire distal lamina (Fig. 9A) and two short bands are located at the base of the lamina (Fig. 9B). Stomata are monocyclic, ellipsoidal, 29-34 μm wide, 45-58 μm long, and have 4-6 subsidiary cells with erect to overarching papillae (Fig. 9C). Epidermal cells may be interspersed with individual stomata in these bands (Fig. 7C). Stomatal bands are separated by a stomatal free zone with numerous papillate epidermal cells and undeveloped papillae (Fig. 9D-9F). Undeveloped papillae appear as flanges on epidermal cells of the stomatal free zone (Figs. 9D-9E). The abaxial surface of the microsporophyll is completely covered by circular trichome bases (Figs. 9G, 9H).

Anatomy of pollen cones and prepollen. Pollen cones have a cone axis bearing helically arranged peltate microsporophylls (Fig. 10A). Six to eight, abaxial, ellipsoidal, pollen sacs are attached to a single area on the shank (Figs. 10B-10C). Many cones only have pollen sac bases preserved, but some are full of monosaccate prepollen grains that conform to the sporae dispersae genus *Potonieisporites* Bharadwaj (1964) (Figs. 10A-10C). Grains are subcircular to circular with a large saccus that surrounds a central body (Figs. 10D-10E). This central body has a proximal monolete suture and parallel folds that are often broken (Figs. 10D-10E). Grains are 91-122 μm long by 71-110 μm wide in polar view.

Ovulate cones. Cones are ellipsoidal, 5.0-8.2 cm long and 1.1-1.6 cm wide, and bear helically-arranged bracts and axillary ovuliferous dwarf shoots (Figs. 11A-11E). These cones can be differentiated from other *Emporia*-like cones in the locality by their greater length, robust morphology, and subtending bracts that are typically longer than axillary dwarf shoots (Figs. 11A-11D), and the presence of axillary dwarf shoots that are as long as the subtending bracts (Figs. 11B-11D). Axillary dwarf shoots diverge from the cone axis at 45° angles and usually have 23-45 sterile scales. Sporophylls are often difficult to see unless the cone is macerated. Some ovulate cones are physically connected to penultimate shoots (Fig. 11A). Leaves on these shoots are simple (Fig. 12A) and similar to those found on penultimate shoots (Table 1).

Bracts. Bracts are forked and have a broad base with numerous marginal trichomes (Fig. 12A). They are narrowly triangular to linear with two tips that taper to a point and a broad base (Fig. 12A, 13A). They have cuticles identical to leaves on vegetative shoots (Table 1). The adaxial surfaces have two bands of stomata, one per forked tip and each band has 2-6 stomata (Fig. 12A). Stomata are ellipsoidal, and have 6-7 papillate subsidiary cells with overarching papillae (Fig. 12C). Leaf margins and stomatal free zones have rectangular epidermal cells with numerous papillae and few or no trichome bases (Figs. 12C). The abaxial surface has two narrow bands of stomata and is entirely covered by trichome bases.

Sterile scales. Sterile scales are triangular to narrowly triangular in face view, S-shaped to slightly S-shaped in side view with a mucronate apex (Figs. 12B, 13D-13H). They are 1.6-6.6 mm long and 0.5-2.0 mm wide. Scales are amphistomatic with two narrow bands of stomata on adaxial and abaxial surfaces (Figs. 12B, 12D). Stomatal complexes have 5-7 papillate subsidiary cells (Fig. 14A-14C). Leaf margins and stomatal free zones have rectangular epidermal cells, few undeveloped papillae, numerous papillae and no trichome bases (Figs. 14B-14D). Papillae on epidermal cells may be short and erect, long and hair-like, or short and wide (Figs. 14D-14F). The abaxial surface is covered completely with surficial trichome bases (Figs. 12D, 13D, 13F).

Morphology and cuticles of sporophylls and ovules. Sporophylls are narrow, 2.6-3.9 mm long and 0.8-1.3 mm wide with a sub-apical , "V" to "U" shaped seed scar (Fig. 14H). They are completely covered by trichome bases (Fig. 14H). Ovules/seeds are bilateral, flattened, with rounded to subcordate bases, and covered with uniseriate trichomes that are often broken (Fig. 14I, 14J).

Anatomy of ovulate cone. The woody cone axis bears bracts that subtend an axillary dwarf shoot with inverted seeds (Figs. 15A-15G). The bract and dwarf shoot diverge as a single unit, but separate almost immediately after diverging from the cone axis. Sections reveal that sterile scales extend from all surfaces along the dwarf shoot, concentrated on the abaxial surface at the apical region of the shoot (Fig. 15A, 15E). Axillary dwarf shoots often have 23-45 sterile scales (Figs. 15A, 15B). The cone axis, as in penultimate shoots, has a large pith with secretory cells with dark contents, and an endarch eustele (Figs.15A-15D). Secondary xylem has radially aligned rows of 4-8 tracheids separated by uniseriate rays (Fig. 15C).

Anatomy of ovules. Ovules are bilaterally symmetrical, inverted, ovoid to ellipsoidal, 3.0-6.0 mm long and 1.0-1.6 mm wide (Figs. 15A-15B, 15F-15G). The micropylar end faces the cone axis and each ovule produces two wings (Figs. 15A, 15B, 15F, 15G). The integument is composed of sarcotesta, sclerotesta and endotesta (Figs.

15F-15G). The sarcotesta is single-layered, while the sclesrotesta is composed of several layers of cells (Figs. 15F-15G). The endotesta is typically single-layered but up to three layers of cells have been observed (Figs. 15F-15G). There is no evidence of vascular tissue in the integument. The nucellus is one-layered and free from the integument except at the micropylar end (Fig. 15G). The nucellus is free from the integument at the micropylar end and shows a nucellar beak (Fig. 15F).

Discussion

Emporia royalii conforms to the general architecture recently determined for walchian conifers (Lausberg 2002; Hernandez-Castillo et al. 2003). These were relatively small plants with plagiotropic lateral branches that produce terminal pollen and ovulate cones. Among primitive conifers, *Emporia royalii* has a novel combination of characters that includes 1) two orders of branching on penultimate shoots, 2) simple and forked, needle-like leaves on penultimate branches (age dependent heterophylly), 3) amphistomatic leaves with two broad adaxial and individual abaxial rows of stomata, 4) adaxial undeveloped papillae on all leaves and leaf-like structures, 5) simple, terminal pollen cones, 6) peltate microsporophylls with adaxial pollen sacs, 7) monosaccate *Potonieisporites* prepollen grains, 8) compound ovulate cones bearing bracts and ovuliferous dwarf shoots, 9) bracts and ovuliferous dwarf shoots fused at the base and separate distally, 10) forked bracts, 11) bilaterally symmetrical ovuliferous dwarf shoots with up to 45 sterile scales interspersed among sporophylls, 12) 1-2 sporophylls per dwarf shoot with slightly recurved apex, 13) one inverted ovule per sporophyll, 14) ovules winged, 15) simple pollen chamber, and 16) nucellar beak.

Almost all of these characters can be found in previously described walchian conifers from Euramerica (Florin 1938-45; Mapes and Rothwell 1984; Kerp et al. 1990; Hernandez-Castillo et al. 2001b; Rothwell and Mapes 2001; Rothwell et al. 2005; chapters 3 and 4 in this dissertation). Nevertheless, *E. royalii* displays a novel combination of characters (Table 2; Florin 1938-45; Mapes and Rothwell 1984; Kerp et al. 1990; Hernandez-Castillo et al. 2001, chapter 3 in this dissertation). *Emporia royalii* is compared to the most completely known "Walchian Voltziales" (Rothwell et al. 2005) at the whole plant species level (Table 2), and at the individual conifer organ level (Tables 3-5) as in previous reconstructions (Rothwell and Mapes 2001; Hernandez-Castillo et al. 2001b, chapters 3 and 4 in this dissertation). These comparisons include vegetative morphological (Table 3), cuticular (Table 4), and ovulate cone/zone (Table 5) characters (Rothwell and Mapes 2001; Hernandez-Castillo et al. 2001b).

Systematic relationships

Whole plant species level. Emporia royalii is similar to other Euramerican "Walchian Voltziales" (Rothwell et al. 2005) in having lateral plagiotropic branches that bear helically arranged, simple, amphistomatic leaves, terminal ovulate cones with bilaterally symmetrical axillary dwarf shoots, small number of ovules per dwarf shoot, and simple pollen cones with adaxial pollen sacs (Table 2). Nevertheless, *E. royalii* differs from most of these taxa by having age dependent heterophylly, amphistomatic leaves with two adaxial bands of stomata, and individual rows of abaxial stomata, and bracts with axillary dwarf shoots that are fused at the base bearing 1-2 interspersed sporophylls (Table 2).

Other taxa such as *Thucydia mahoningensis* Hernandez-Castillo, Rothwell et

Mapes and *Barthelia furcata* Rothwell et Mapes differ greatly from *E. royalii* by having irregular branching (*B. furcata*), no heterophylly (*T. mahoningensis*) or size dependent heterophylly (*B. furcata*), only adaxial stomata, and fertile zones instead of terminal ovulate cones (Tables 2, 5). Moreover, *T. mahoningensis* has compound pollen cones instead of simple pollen cones as in other conifers (Table 2).

Emporia royalii is most similar to other species of the Emporiaceae (Table 2). *Emporia cryptica* Hernandez-Castillo, Stockey, Rothwell and Mapes differs from *E. royalii* by having simple leaves on penultimate shoots, no heterophylly, and narrow abaxial bands of stomata (Table 2). Meanwhile, *E. lockardii* only differs from *E. royalii* by having abaxial rows of stomata, axillary dwarf shoots that are completely separate throughout from the bracts, and 1-3 sporophylls per dwarf shoot (Table 2). The number of sporophylls in *E. lockardii* is 1-3 and its range overlaps with that of *E. royalii*, and as does the stomatal distribution of leaves on ultimate shoots (Table 2). Furthermore, *E. lockardii* is the only conifer with age dependent heterophylly known thus far (Table 2; chapter 3 in this dissertation). *Emporia royalii*, then, is most similar to *E. lockardii* but its unique combination of characters put this plant within the genus *Emporia* as a new species.

Individual organ comparisons. Morphological characters of leaves on penultimate and ultimate shoots in all these conifers overlap considerably when length, width, and shape are compared to *E. royalii* (Table 3). Of these, only length in leaves of penultimate shoots provide an accurate way to differentiate species based on leaf characters (Table 3). *Emporia royalii* is the conifer with the smallest leaves on penultimate shoots followed by *Otovicia hypnoides* (Florin) Kerp, Swinkels, and Verweer (Table 3).

Cuticular characters from leaves on ultimate shoots traditionally have been used to differentiate among species of walchian conifers (Florin 1938-45, 1951; Clement-Westerhof 1984; Visscher et al. 1986; Lausberg and Kerp 2000). Most of these conifers have amphistomatic leaves with bands of stomata with the exception of *Hanskerpia hamiltonensis* Rothwell, Mapes and Hernandez-Castillo (Rothwell et al. 2005) and *Ernestiodendron filiciforme* Florin (Florin 1938-45), which have amphistomatic leaves with parallel rows of stomata (Table 4). All of them display similar combinations of marginal trichomes, abaxial trichome bases, and papillate epidermal cells (Table 4). However, differences among taxa can be seen in the presence or absence of adaxial trichome bases. Traditional characters such as the size and number of subsidiary cells per stomata are, in general, confusing and they overlap in most taxa (Table 4). Stomatal size is not a reliable character because no standard rules for measuring stomata and stomatal complex size may be influenced by the position of the stomata on the leaf (e.g., apical vs. basal stomata).

Moreover, cuticular variation within a single plant may show dissimilar stomatal distribution, number of stomata per band or even number of subsidiary cells in different organs from the same plant (Tables 1, 4). To solve this problem, a complete cuticular survey of the different organs in complete walchian plants must be undertaken in order to differentiate isolated and/or fragmentary conifers based on their cuticular features. Walchian plant identification and or typification cannot rely solely on the study of in situ or dispersed cuticles (chapter 4 in this dissertation). A combination of numerous specimens and multiple characters is needed to accurately identify these conifers as complete plants.

Ovulate cone characters play an important role in walchian conifer systematics and they are often used to characterize conifer families (Florin 1938-45, 1950; 1951; Clement-Westerhof 1984, 1987, 1988; Kerp et al. 1990; Kerp and Clement-Westerhof 1991; Mapes and Rothwell 1991, 2003; Hernandez-Castillo et al. 2001b; Rothwell and Mapes 2001, 2003; Rothwell et al. 2005). Diagnostic ovulate cone characters are reduced to the position and nature of the cone or zone, bract morphology, dwarf shoot symmetry, and sporophyll position and number (Table 5; see Hernandez-Castillo et al. 2001b) and they are useful to differentiate among major clades of primitive conifers (Hernandez-Castillo et al. 2001b; Rothwell et al. 2005; chapter 3 in this dissertation). However, they are not very useful when walchian Voltziales are the only taxa compared (Table 5). From these characters, only the number of sterile scales per axillary dwarf shoot and position and number of sporophylls are useful to differentiate individual species (Table 5). The number of sterile scales is similar among most taxa, but is diagnostic in the Emporiaceae (Table 5). The number of sporophylls per dwarf shoot overlaps tremendously among all taxa (Table 5) and it ranges from 1-4 (Table 5). Therefore, ovulate cone characters have to be combined with other characters from the rest of the plant to address familial, generic, and ultimately phylogenetic relationships.

Emporiaceae at the Hamilton Quarry. Emporia royalii reveals another novel combination of characters among walchian conifer species, and is now added to the growing list of complete fossil conifer reconstructions from the Paleozoic (Hernandez-Castillo et al. 2001b; Rothwell and Mapes 2001; Rothwell et al. 2005; chapters 3 and 4 in this dissertation). Several families of walchian conifers and related coniferophytes are known (i.e., Walchiaceae sensu Clement-Westerhof 1984; Emporiaceae Mapes and Rothwell 1991, 2003; Utrechtiaceae Mapes and Rothwell 1991, Rothwell and Mapes 2003; Bartheliaceae, Rothwell and Mapes 2001; Thucydiaceae, Hernandez-Castillo et al. 2001b). From these, the Emporiaceae is the only family that is based on morphological, cuticular, and anatomical characters (Rothwell et al. 2005; chapters 3 and 4 in this dissertation), and the only family of fossil conifers where all its members are characterized as complete plants.

The Emporiaceae comprises two genera and four species. The genus *Emporia* has three species (*E. lockardii*, *E. cryptica*, *E. royalii*) while *Hanskerpia* is a monotypic genus (*Hanskerpia hamiltonensis*). These are typical small stature walchian conifers with lateral plagiotropic branches. Although, *E. cryptica* is the only species described with an antepenultimate shoot attached to lateral branches, we assume that the rest of the species had a similar growth architecture based on the size and shape of lateral branches (Hernandez-Castillo et al. 2003, chapters 3 and 4 in this dissertation). Two of these species, *E. lockardii* and *E. royalii*, have position- and size-dependent heterophylly that has been characterized as age-dependent heterophylly (chapter 3 in this dissertation). Age-dependent heterophylly in Emporiaceae refers to the presence of simple leaves on small diameter (young) penultimate shoots (from small to medium sized lateral branches), in contrast to the presence of forked leaves on large diameter (mature) lateral branches (usually at the base of ovulate cones).

Another growth architectural resemblance of Emporiaceae to living araucarians is shown by *E. royalii*. *Emporia royalii* has large lateral branches with ultimate shoots that are all oriented in the same direction (dihedral arrangement, Veillon 1978) that resemble branches of *Araucaria heterophylla* (Salisb.) Franco or *Araucaria bernieri* Buchholz (Veillon 1978; Hernandez-Castillo pers. obs.). This type of branch is commonly found in the middle and apical regions of mature *A. heterophylla* trees (Hernandez-Castillo pers. obs.) and other species in the same genus that have a Massart tree architecture model (Veillon 1978). This suggests that two of the typical growth architectural features of living *A. heterophylla* trees (age-dependent heterophylly and "upright" branches) were already present in the Emporiaceae during the Paleozoic.

These findings are very important because they confirm that Carboniferous conifers were already experimenting with growth architecture and developmental patterns commonly found in living representatives of the Araucariaceae and other living conifers (de Laubenfels 1972; Veillon 1980; Grosfeld et al. 1999; Hernandez-Castillo 2003; Hernandez-Castillo pers. obs.). As such, it seems probable that we will find younger conifers (Permian) with architecture more similar to that of living conifers. At least a single compression/impression specimen of an incomplete lateral branch from an unknown Permian locality from the Massif Centrale of France, appears to have leaves comparable to those of mature trees of *A. heterophylla* (Hernandez-Castillo pers. obs.), suggesting the presence of taller trees with a different leaf morphology in the Permian of Euramerica. If more specimens are located to confirm this preliminary idea, it would suggest that this Permian conifer had already undergone an extended delay in the onset of reproductive maturity, and a subsequent change in leaf morphology associated with an more extended period of growth (McNamara, 1986; Hernandez-Castillo et al. 2003).

The Emporiaceae is the only family where all cuticles of leaves and leaf-like structures have been fully analyzed. Cuticular features of these species show that all leaves of a single plant have a basic stomatal structure, distribution, number of stomata per band, and number of subsidiary cells per stoma (Table 1), but this basic pattern varies among the different organs of the plant (Table 1; chapters 3-4 in this dissertation). This confirms that cuticles from isolated and/or fragmentary branches, where no organic connections and/or small number of specimens are known, are not useful in accurately identifying walchian conifer plants.

Pollen cones in the Emporiaceae are terminal on ultimate shoots and simple where a cone axis bears a series of helically-arranged microsporophylls (Mapes and Rothwell 1998; Rothwell et al. 2005; chapters 3 and 4 in this dissertation). They contrast with living families in having pollen sacs attached to the adaxial surface of the shank (Mapes and Rothwell 1998; Rothwell et al. 2005; chapters 3 and 4 in this dissertation). The number of pollen sacs ranges from 4-14 in the family and they contain monosaccate, prepollen grains of the sporae dispersae genus *Potonieisporites* Bharadwaj (1964). Taggart and Ghavidel-Syooki (1988) described three prepollen types (*P. neglectus* Potonié et Lele, *P. granulatus* Bose et Kar, and an unknown species) from the Hamilton Quarry locality but these cannot be accurately correlated to pollen cones of individual species due to their rather similar morphology and size (chapters 3 and 4 in this dissertation). Variation among these grains is equivalent to that surveyed by Bharadwaj (1964) and it needs to be analyzed in more detail among these conifer species.

Ovulate cones in the family show that these conifers had a single inverted ovule per sporophyll (Mapes and Rothwell 1984; Rothwell et al. 2005; chapters 3-4 in this dissertation), a bilaterally symmetrical axillary dwarf shoot with distinct bracts and sterile scales. Prepollen and micropyle size also suggests that pollination in these conifers is equivalent to that of conifers with saccate pollen and a pollination-drop mechanism (Owens and Blake, 1983; Owens et al., 1987; Runions et al., 1999; Tomlinson and Takaso, 2002; chapter 4 in this dissertation).

Both vegetative and fertile organs of Emporiaceae species support a basal clade of "Walchian Voltziales" from Euramerica (Rothwell et al. 2005) with characteristics that are found among families of extant conifers. At the same time, they have characters not found in their extant counterparts such as 1) trees of small stature with determinate lateral branches, 2) amphistomatic leaves with bands of monocyclic, incompletely dicyclic, and/or dicyclic stomata, and abaxial surfaces covered with numerous surficial trichomes, 3) simple pollen cones with many adaxially attached pollen sacs, 4) monosaccate, eusaccate, prepollen grains, 5) compound ovulate cones with bracts and axillary dwarf shoots bearing interspersed narrow sporophylls with many sterile scales, and 6) sporophylls with a single inverted ovule.

Even though more than 70 species of walchian conifers have been described worldwide (Florin 1938-45, 1940, 1951, 1964; Clement-Westerhof 1984, 1987, 1988; Mapes and Rothwell 1984, 1991, 2003; Winston 1984; Cuneo 1985; Visscher et al. 1986; Archangelsky and Cuneo 1987; Kerp et al. 1990, 1996; Kerp and Clement-Westerhof 1991; Galtier et al. 1992; Broutin and Kerp 1994; Freytet et al., 1996; Meyen 1997; Hernandez-Castillo et al. 2001b; Rothwell and Mapes 2001; Lausberg 2002; Rothwell et al. 2005; chapters 3 and 4 in this dissertation) we only know a handful of these taxa as complete plants. More conifers need to be reconstructed to understand how the most primitive conifers are related to other fossil (Mesozoic, Cenozoic) and living conifers. Knowledge of the morphological, cuticular, anatomical, growth architectural and reproductive characters of these conifers will help us to understand conifer variation and character recognition. This will allow for a more accurate coding for future phylogenetic analyses of both fossil and extant conifers.

Emporia royalii is the fifth conifer reconstructed from the Hamilton Quarry (Rothwell and Mapes 2001; Rothwell et al. 2005; chapters 3 and 4 in this dissertation). These constitute the largest number of conifers ever reconstructed from a single locality in the world at any age in the fossil record. Four species, *E. royalii*, *E. cryptica*, *E. lockardii* and *H. hamiltonensis* belong to the family Emporiaceae (Mapes and Rothwell 1991, 2003; chapters 3-4 in this dissertation) and the fifth species, *B. furcata*, belongs to Bartheliaceae (Rothwell and Mapes, 2001). Thus, the Emporiaceae is the best known family of walchian conifers from the Paleozoic and the best known family of fossil conifers in the world. These reconstructions are part of a broader study to reinvestigate, describe, and reevaluate morphological characters, and species of Euramerican Paleozoic walchian conifers. The Hamilton Quarry whole plant reconstructions and other conifer reconstructions will be used in the near future to try to resolve systematic relationships among fossil and living conifers.

Table 1. Comparison of morphological and cuticular characters of leaves on vegetative and fertile organs of *Emporia royalii* sp. nov.

Organs/ Characters	Shape (face view)	Shape (side view)	Length (mm)	Width (mm)	Stomata				Papillae		Trichome bases (adx / abx)
					Structure	Distribution (adaxial / abaxial)	Number of stomata per band	Subsidiary cell number	Subsidiary cells	Epidermal cells	
Leaves on penultimate shoots	Nt, Li, Fr	Ss, Sss	1.6 - 5.0	0.3 - 1.5	Monocyclic, stom plug	Two long bands / two ind. rows to narrow bands	2 - 6	5 - 6	Overarching	Abundant	None, Few / abundant
Leaves on ultimate shoots	Nt, Li	Sc, Sss	1.6 - 4.5	0.6 - 1.7	Monocyclic, stom plug	Two long bands / two ind. rows	2 - 8	6 - 8	Erect, overarching	Abundant	None / abundant
Leaves on branches with attached to pollen cones	Nt, Li	Sc, Sss	1.2 -2.5	0.3 - 1.4	Monocyclic, stom plug	Two long bands / two ind. rows	2 - 8	6 - 8	Overarching	Abundant	None / abundant
Microsporophylls	Nt	Sc	0.25 - 4.1	2.0 - 2.6	Monocyclic, stom plug	Two long bands / none or few scattered	2 - 4	4 - 6	Erect, overarching	Abundant	None / abundant
Leaves on branches with attached to ovulate cones	Nt, Li, Fr	Ss, Sss	1.7 - 5.0	0.4 - 1.4	Monocyclic, stom plug	Two long bands / two ind. rows to narrow bands	2 - 6	5 - 6	Overarching	Abundant	None, Few / abundant
Bracts of ovulate cones	Nt, Li, Fr	Li, Sc	1.6 - 2.1	2.1 - 4.0	Monocyclic, stom plug	Two long bands / two ind. rows to narrow bands	2 - 6	6 - 7	Overarching	Abundant	None / abundant
Sterile scales of ovulate cones	Tr, Nt	Ss, Sss	1.6 - 7.6	0.5 - 2.0	Monocyclic, stom plug	Two long bands / two ind. rows to narrow bands	1 - 2	5 - 7	Erect	Abundant	None / abundant

Leaf shape abbreviations: Fr = Forked Tip, Li = Linear, Nt = Narrowly triangular, Sc = Slightly concave, Ss = S-shaped, Sss = Slightly S-shaped, Tr= Triangular, stom plug= stomatal plugs._

Table 2. Comparison of morphological and cuticular characters of *Emporia royalii* sp. nov. and other Paleozoic conifers and coniferophytes. Characters that differ from those of *E. royalii* are recorded in bold face type.

Species/ Characters	**Lateral branches**	**Penultimate leaves**	**Ultimate leaves**	***Hetero phylly**	**Stomatal distribution (vegetative leaves)**	**Stomatal pattern Adx / Abx**	**Compound ovulate organ**	**Bract and ovuliferous dwarf shoot**	**Sporophyll position / number**	**Pollen Cone**	**Microsporophylls**	**Pollen Sacs**
Emporia royalii	Plagiotropic	Simple and forked	Simple	Age and position dependent	Amphistomatic	Two bands / ind. rows	Cone	Fused at base	Interspersed with SS, 1-2	Simple	Simple	Adaxial
Emporia cryptica	Plagiotropic	**Simple**	Simple	**Absent**	Amphistomatic	Two bands / **narrow bands**	Cone	Fused at base	Interspersed with SS, 2	Simple	Simple	Adaxial
Emporia lockardii	Plagiotropic	Simple and forked	Simple	Age and position dependent	Amphistomatic	Two bands / **two short, narrow,** ind. rows	Cone	**Separate throughout**	Interspersed with SS, 1-3	Simple	Simple	Adaxial
Hanskerpia hamiltonensis	Plagiotropic	**Forked**	Simple	**Position dependent**	Amphistomatic	**Parallel rows / parallel rows**	Cone/zone?	Fused at base	Interspersed with SS, 1-2	?	?	?
Thucydia mahoningensis	Plagiotropic	**Simple**	Simple	**Absent**	**Adaxial**	Two bands / **absent**	**Fertile zone**	**Separate throughout**	**Terminal, 3-4**	**Compound**	Simple	**Terminal**
Utrechtia floriniformis	Plagiotropic	**Forked**	Simple	**Position dependent**	Amphistomatic	Two bands / **two bands**	Cone	**Separate throughout**	**Terminal, 1**	Simple	Simple	Adaxial
Otovicia hypnoides	Plagiotropic	**Forked**	Simple	**Position dependent**	**Primarily adaxial**	Two bands / **scattered**	Cone	**Separate throughout**	Interspersed with SS, 2	Simple	Simple	Adaxial
Ernestiodendron filiciforme	Plagiotropic	**Simple**	Simple	**Absent**	Amphistomatic	**Parallel rows / parallel rows**	Cone	**Separate throughout**	**Terminal, 1**	Simple	Simple	?
Barthelia furcata	**Irregular**	**Forked**	**Simple & forked**	**Size dependent**	**Adaxial**	Two bands / **absent**	**Fertile zone**	**Separate throughout**	Interspersed with SS, ?	Simple	**Forked**	Adaxial

Modified from Rothwell et al.2005. * Heterophylly is based on differences in the shape of leaves, where two distinctive types of leaves are known. Adx = adaxial, Abx =abaxial, SS = sterile scales.

Table 3. Comparison of leaves using morphological characters of *Emporia royalii* sp. nov. Characters that differ from those of *E. royalii* are recorded in bold face and overlapping characters are recorded in italics.

Species/ Characters	Stem	Lateral branches	Penultimate leaves				Ultimate leaves						*Heterophylly
			Length (mm)	Width (mm)	Shape (face view)	Shape (side view)	Length (mm)	Width (mm)	Shape (face view)	Shape, (side view)	Angle of Divergence Base	Apex	
Emporia royalii	Orthotropic?	Plagiotropic	1.6-5.0	0.3.-1.5	Nt, Li, Fr	Ss, Sss	1.6-4.5	0.6-1.7	Nt, Li	Sc, Sss	24-57	21-61	Present
[0]*Emporia cryptica*	Orthotropic	Plagiotropic	*2.4-7.1*	*0.6-2.0*	*Nt, Li*	*Ss*, Sp	*1.2-2.7*	*0.3-1.2*	Nt, Li	*Sss, Sc,* Sp	*30-64*	*27-70*	*Present*
[1]*Emporia lockardii*	Orthotropic?	Plagiotropic	*5.0-10.0*	*1.0-2.1*	Nt, Li, Fr	*Sc, Sss*	*1.7-5.0*	0.4-1.16	Nt, Li	Sc, Sss	*26-63*	*28-69*	Present
[2]*Hanskerpia hamiltonensis*	Orthotropic?	Plagiotropic	13-29	*1.0-1.74*	*Li, Fr*	Sp	5-15	*0.6-1.1*	*Li*	*Sc,* Sp	*30-45*	*32-50*	Present
[3]*Thucydia mahoningensis*	Orthotropic	Plagiotropic	5.0-12.5	*1.0-1.5*	*Nt, Li*	Sc, *Ss*	*3-6*	*0.4-1.0*	Nt, Li	[a]Sc, Ss		*21-54*	Absent
[4]*Utrechtia floriniformis*	Orthotropic?	Plagiotropic	12.0-25.0	*1.5-3.0*	Nt, Li, Fr	Sc	9-13	*0.4-0.6*	Nt, Li	*Sc,* Ss	?	*30*	Present
[5*]*Lebachia garnettensis*	?	Plagiotropic	*3.0-16.0*	*1.5-2.5*	*Nt, Li*	Sc	*4.0-7.0*	*0.4-1.4*	Nt, Li	*Sc,* Ss	*35-70*	?	Absent
[6]*Otovicia hypnoides*	?	Plagiotropic	*2.0-8.0*	*1.0-1.5*	St, La, *Fr*	[c] Fa, *Ss*	*1.5-4.0*	0.2-0.5	Nt, Li	[c] Fa	*35-90*	*35*	Present
[2]*Ernestiodendron filiciforme*	?	Plagiotropic	10.0-23.0	*1.5-3.5*	*Nt, Li*	[b]Sc, Sp	7-15	*1.5-2.0*	Nt, Li	Sp	70-110	15	Absent
[7]*Barthelia furcata*	?	Irregular	22-47	<4.0	*Li, Fr*	Li, Sc	10-25	<4.0	Li	Li, *Sc*	*25-35*	*14-25*	Present

Modified from Hernandez-Castillo et al., 2001b. [0] Hernandez-Castillo et al 2005b. [1] Including measurements of Mapes and Rothwell, 1984, 1991. [2] Florin 1938-45. [3] Hernandez-Castillo et al 2001 b. [4] Mapes and Rothwell 1991. [5*] Emended by Winston (1984). [6] Kerp et al. 1990; however, leaf measurements were taken from Florin (1938-45) because such data are not available in Kerp et al. 1990. [7] Rothwell and Mapes 2001.

Leaf shape abbreviations: El = Elliptical, Fr = Forked Tip, Li = Linear, Ns= Narrow sub-triangular, Nt = Narrowly triangular, Ob= Oblong, Ov= Ovate, Sc = Slightly concave, Sl= Slightly lanceolate, Sp= Spreading, Sq= Squamose (=scale like), Ss = S-shaped, Sss = Slightly S-shaped, St= Sub-triangular, Tr= Triangular. * Heterophylly is based on differences in the shape of leaves, where two distinctive types of leaves are known. a, b, and c refer to leaf shape definitions according to table 2 of Hernandez-Castillo 2001b.

Table 4. Comparison of cuticular features of leaves on ultimate shoots of *Emporia royalii* sp nov. and other Paleozoic conifers. Characters that differ from those of *E. royalii* are recorded in bold face and overlapping characters are recorded in italics.

Species/ Characters	Stomatal distribution adaxial	Stomatal distribution abaxial	Stomatal complex structure	Stomatal complex size (µm)	Subsidiary cell number	Subsidiary cell papillae	Marginal trichomes	Trichome bases adaxial	Trichome bases abaxial	Epidermal papillae adaxial	Epidermal papillae abaxial
Emporia royalii	Two long bands	Few, ind. rows	Monocyclic	55 x 68	6 - 8	Present	Present, short and long	Present	Present abundant	Present	Present
[0] *Emporia cryptica*	Two long bands	**Two narrow bands**	*Monocyclic*, **Dicyclic**	53 x 44	*5 - 8*	Present	Present, short and long	Present abundant	Present, abundant	Present	Present
[1] *Emporia lockardii*	Two long bands	**Two short, narrow,** *ind. rows*	Monocyclic	58 x 46	*5 - 9*	Present	Present, short and long	**Few or absent**	Present abundant	Present	Present
[2] *Hanskerpia hamiltonensis*	**Parallel rows**	**Parallel rows**	Monocyclic	30 x 70	*5 - 6*	Present	*Present, short*	*Present*	Present abundant	Present	Present
[3] *Thucydia mahoningensis*	Two long bands	**Absent**	Monocyclic	24 x 20	*6 - 8*	Present	*Present, large, short,* **hair-like**	**Absent**	Present, abundant	Present	**Absent**
[4] *Utrechtia floriniformis*	Two long bands	**Two short bands, variable**	Monocyclic	50 x 55	*5 - 9*	Present	*Present, short,* **hair-like**	*Present*	Present, abundant	Present	Present
[5] *Lebachia garnettensis*	Two long bands	*Few,* **scattered**	Monocyclic	[8]45 x 40	**More than 10?**	**Absent**	*Present, short,* **hair-like**	**Absent**	Present abundant	?	?
[6] *Otovicia hypnoides*	Two long bands	**Few stomata groups**	*Monocyclic,* **inc dicyclic**	70 x 60	5 - 8	Present	*Present,* **conical**	*Present*	Present abundant	Present	Present
[2] *Ernestiodendron filiciforme*	**Parallel rows**	**Parallel rows**	*Monocyclic,* **inc dicyclic**	[8]60 x 40	4 - 8	Present	*Present, short,* **hair-like**	*Present*	Present abundant	**Absent**	Present
[7] *Barthelia furcata*	Two long bands	**Absent**	Monocyclic	36 x 63	4 - 7	Present	*Present, short,* hair-like	*Present*	Present, abundant	Present	Present

Modified from Hernandez-Castillo et al., 2001b.[0] Hernandez-Castillo et al 2005b. [1] Mapes and Rothwell, 1984, 1991. [2] Florin 1938-45. [3] Hernandez-Castillo et al 2001 b. [4] Mapes and Rothwell 1991. [5+] Emended by Winston (1984). [6] Kerp et al 1990; however, leaf measurements were taken from Florin (1938-45) because such data are not available in Kerp et al 1990. [7] Rothwell and Mapes 2001. [8] Measured directly from Florin's monograph (1938-45). Dicyclic = dicyclic stomata, inc dicyclic= incompletely dicyclic stomata.

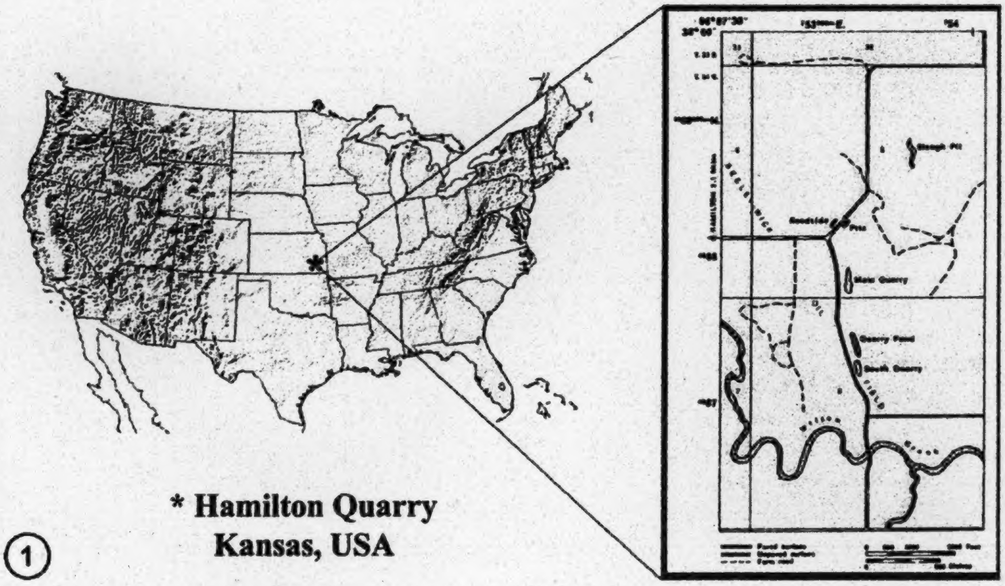
Table 5. Characters of compound ovulate cones and zones of *Emporia royalii* sp. nov. and those of other Paleozoic conifers. Characters that differ from those of *E. royalii* are recorded in bold face and overlapping characters are recorded in italics.

Species/ Characters	Ovulate fructification	Cone Morphology			Bract	Dwarf shoot				Ovules
		Length (cm)	Width (cm)	Shape		Symmetry	Number of sterile scales	Position of sporophylls	Number of sporophylls*	
Emporia royalii	Terminal cone	5.0-8.2	1.1-1.6	Cylindrical to ellipsoidal	Forked	Bilateral	>40	Interspersed with SS	1 - 2	Terminal, Inverted
[0] *Emporia cryptica*	Terminal cone	*5.0-6.2*	*0.7-1.2*	*Ellipsoidal*	Forked	Bilateral	**20-25**	Interspersed with SS	*2*	Terminal, Inverted
[1] *Emporia lockardii*	Terminal cone	**2.8-5.0**	*1.1-1.5*	Cylindrical to ellipsoidal	Forked	Bilateral	**14-30**	Interspersed with SS	*1 - 3*	Terminal, Inverted
[2] *Hanskerpia hamiltonensis*	**Terminal cone/zone?**	**11.0**	**2.7**	Cylindrical	Forked	Bilateral	**<15?**	Interspersed with SS	1 - 2	Terminal, Inverted
[3] *Thucydia mahoningensis*	**Fertile Zone**	**3.0-4.5**	*0.9-1.5*	Cylindrical to ellipsoidal	**Simple**	Bilateral	**10-15**	**Terminal**	**3 - 4**	Terminal, Inverted
[4] *Utrechtia floriniformis*	Terminal cone	**7.0**	*1.2*	Cylindrical to ellipsoidal	Forked	Bilateral	**>10**	**Terminal**	*1*	Terminal, Inverted
[5] *Lebachia garnettensis*	Terminal cone	**2.0-3.0**	**0.10-0.15**	*Ellipsoidal*	Forked	Bilateral	**<5?**	?	***≥3?**	?
[6] *Otovicia hypnoides*	Terminal cone	**3.0-6.5**	*1.1-1.8*	Cylindrical	Forked	Bilateral	**>10**	Interspersed with SS	*2*	Terminal, Inverted
[2] *Ernestiodendron filiciforme*	Terminal cone	**10.0-20.0**	**2.2-3.0**	*Ellipsoidal*	Forked	Bilateral	**5-10**	**Terminal?**	*1*	Terminal, Inverted
[7] *Barthelia furcata*	**Fertile zone**	**Up to 16**	**2.4-2.6**	Cylindrical to ellipsoidal	Forked	**Radial**	**?**	**Terminal**	?	Terminal, Inverted?

Modified from Hernandez-Castillo et al., 2001b. [0] Hernandez-Castillo et al 2005b. [1] Mapes and Rothwell, 1984, 1991. [2] Florin 1938-45. [3] Hernandez-Castillo et al 2001 b. [4] Mapes and Rothwell 1991. [5+] Emended by Winston (1984). [6] Kerp et al 1990; however, leaf measurements were taken from Florin (1938-45) because such data are not available in Kerp et al 1990. [7] Rothwell and Mapes 2001. [8] Meyen, 1997, angles estimated from plates. * Fertile scale as in Florin, Clement-Westerhof (1984) and Kerp et al. (1990) concepts. SS= sterile scales.

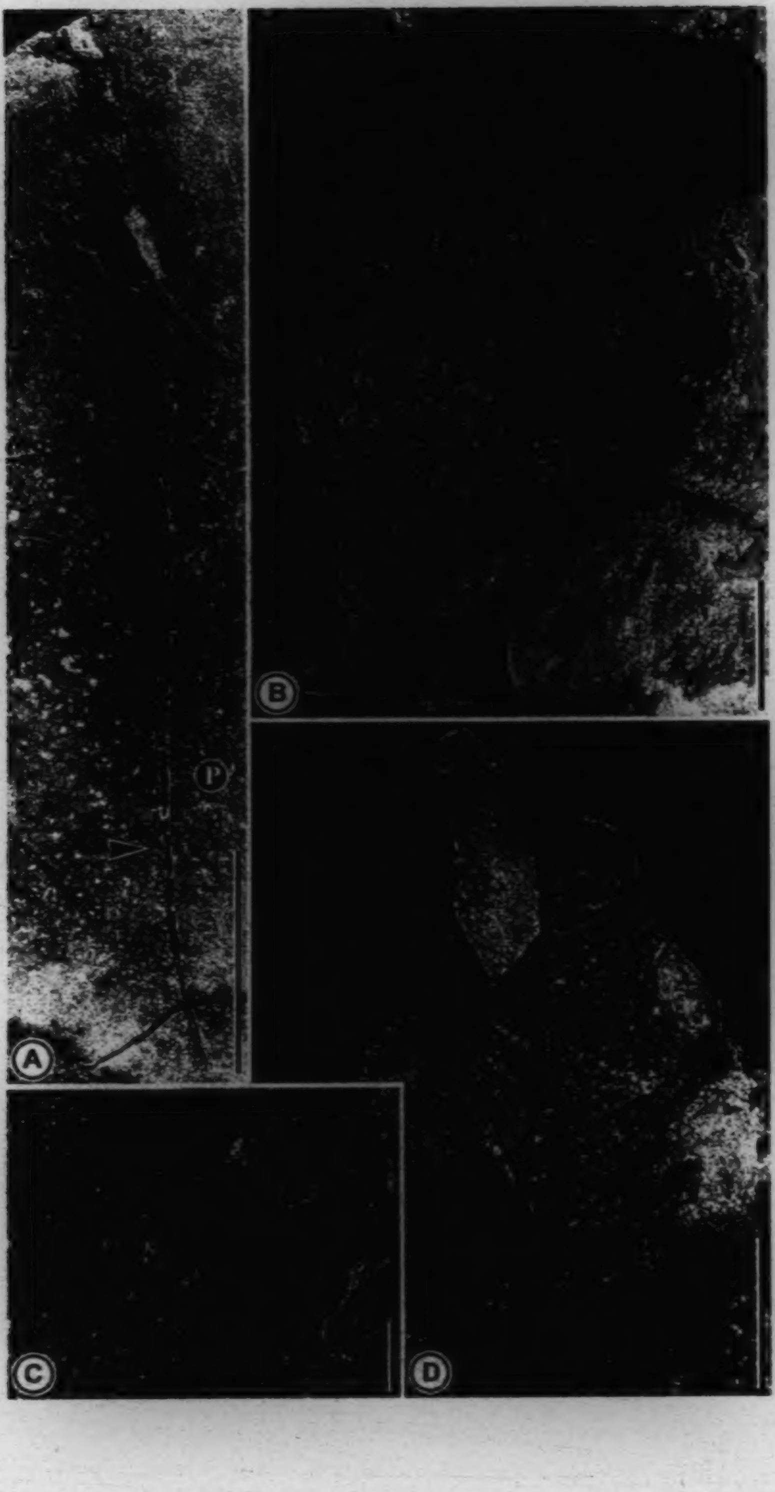
Figure Captions

Fig. 1. Map showing location of the Hamilton Quarry locality, Kansas, USA.


96°07'30"
38°00'
53000m E.
54
Slough Pit
Roadside Pit
Main Quarry
Quarry Pond
South Quarry

① *** Hamilton Quarry**
Kansas, USA

Figs. 2A-D. *Emporia royalii* sp. nov., lateral branches. **A.** Penultimate shoot (p) with leaves (arrowhead), and ultimate shoots. M 1618, scale bar = 10 cm. **B.** Ovoid branch showing penultimate shoot and ultimate shoots with helically arranged leaves on ultimate shoots. M 4021 A, scale bar = 2 cm. **C.** Branch showing slightly concave leaves. M 4018, scale bar = 2 cm. **D.** Deltoid branch with large ultimate shoots. M 4020, scale bar = 5 cm.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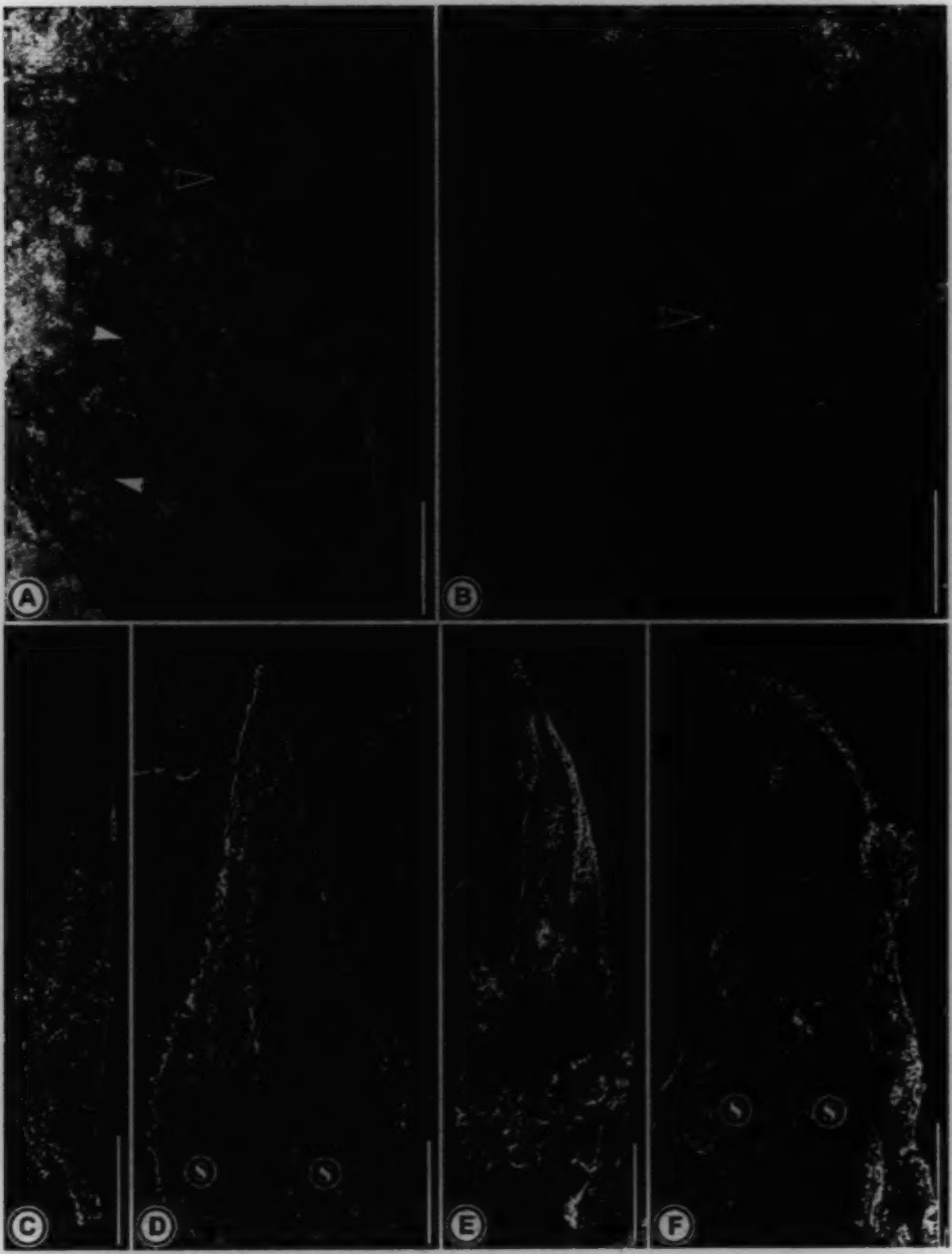
Figs. 3A-F. *Emporia royalii* sp. nov., lateral branches and SEM of leaves. **A.** Branch showing leaves on penultimate shoots (white arrowheads) and slightly concave to S-shaped leaves of ultimate shoots. M 1626 A, scale bar = 1 cm. **B.** Branch showing leaves on penultimate (arrowhead) and ultimate shoots. M 2618, scale bar = 1 cm. **C.** Side view of slightly S-shaped leaf on penultimate shoot. M 1627, scale bar = 1 mm. **D.** Triangular leaf of ultimate shoot showing marginal trichomes and adaxial bands of stomata (s). M 1627, scale bar = 0.5 mm. **E.** Side view of slightly concave leaf from ultimate shoot. M 1627, scale bar = 0.5 mm. **F.** Side view of leaf from ultimate shoot showing adaxial bands of stomata (s). M 1627, scale bar = 0.5 mm.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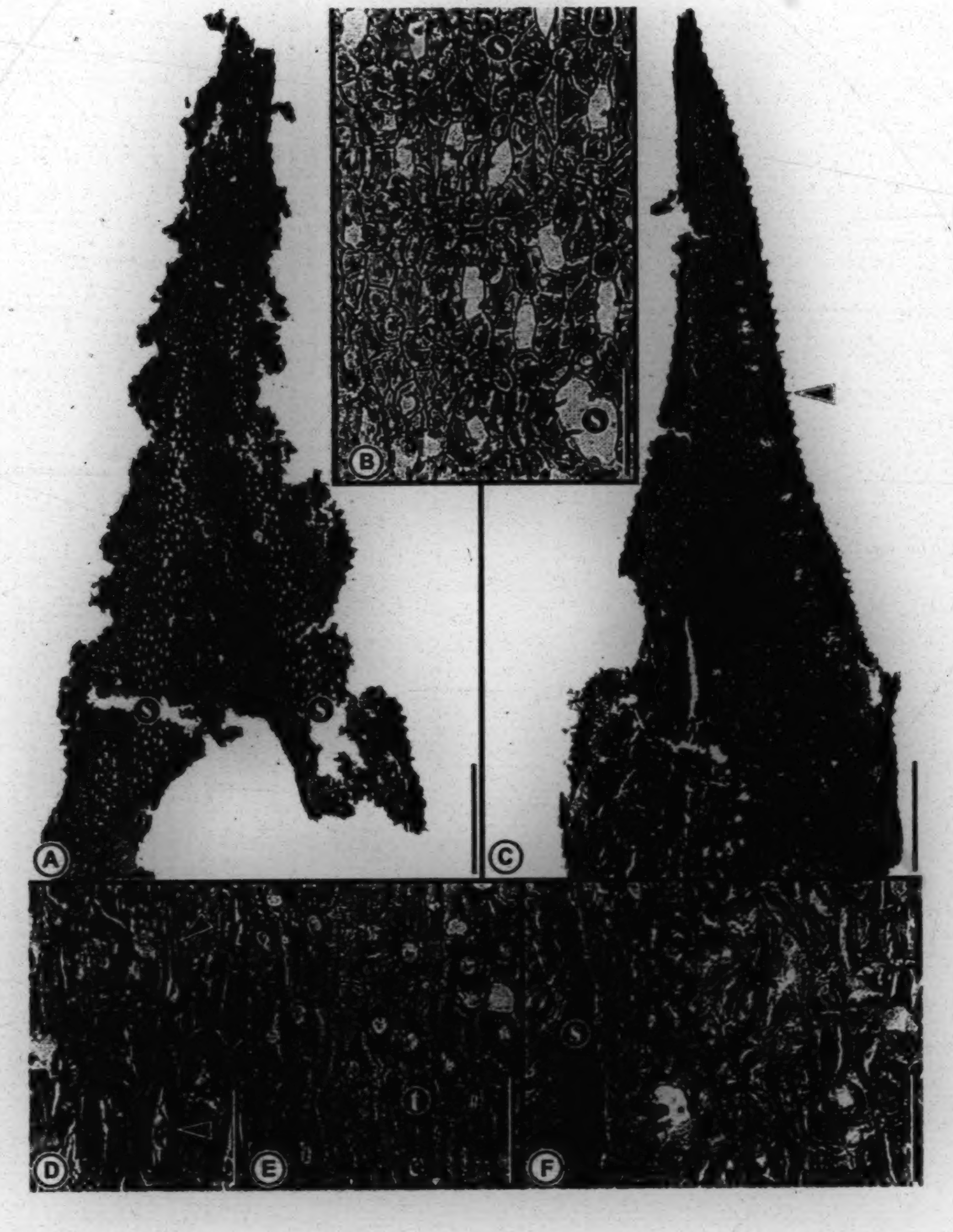
Figs. 4A-F. *Emporia royalii* sp. nov., cuticular macerations of leaves on penultimate shoots. All specimens macerated from M 1626. **A.** Leaf from penultimate shoot showing narrowly triangular shape and two adaxial bands of stomata (s) separated by stomatal central free zone. Scale bar = 0.5 mm. **B.** Penultimate leaf showing adaxial papillate epidermal cells (left) and stomatal band (s). Scale bar = 60 μm. **C.** Narrowly triangular leaf showing abaxial surface and marginal trichomes. Scale bar = 0.5 mm. **D.** Adaxial stomatal free zone showing elongated epidermal cells and fused papillae on undeveloped papillae. Scale bar = 10 μm. **E.** Penultimate leaf showing abaxial trichome bases (t) and elongated epidermal cells. Scale bar = 40 μm. **F.** Abaxial stomatal narrow band showing stomatal complexes (S) with subsidiary cells and overarching papillae. Scale bar = 40 μm.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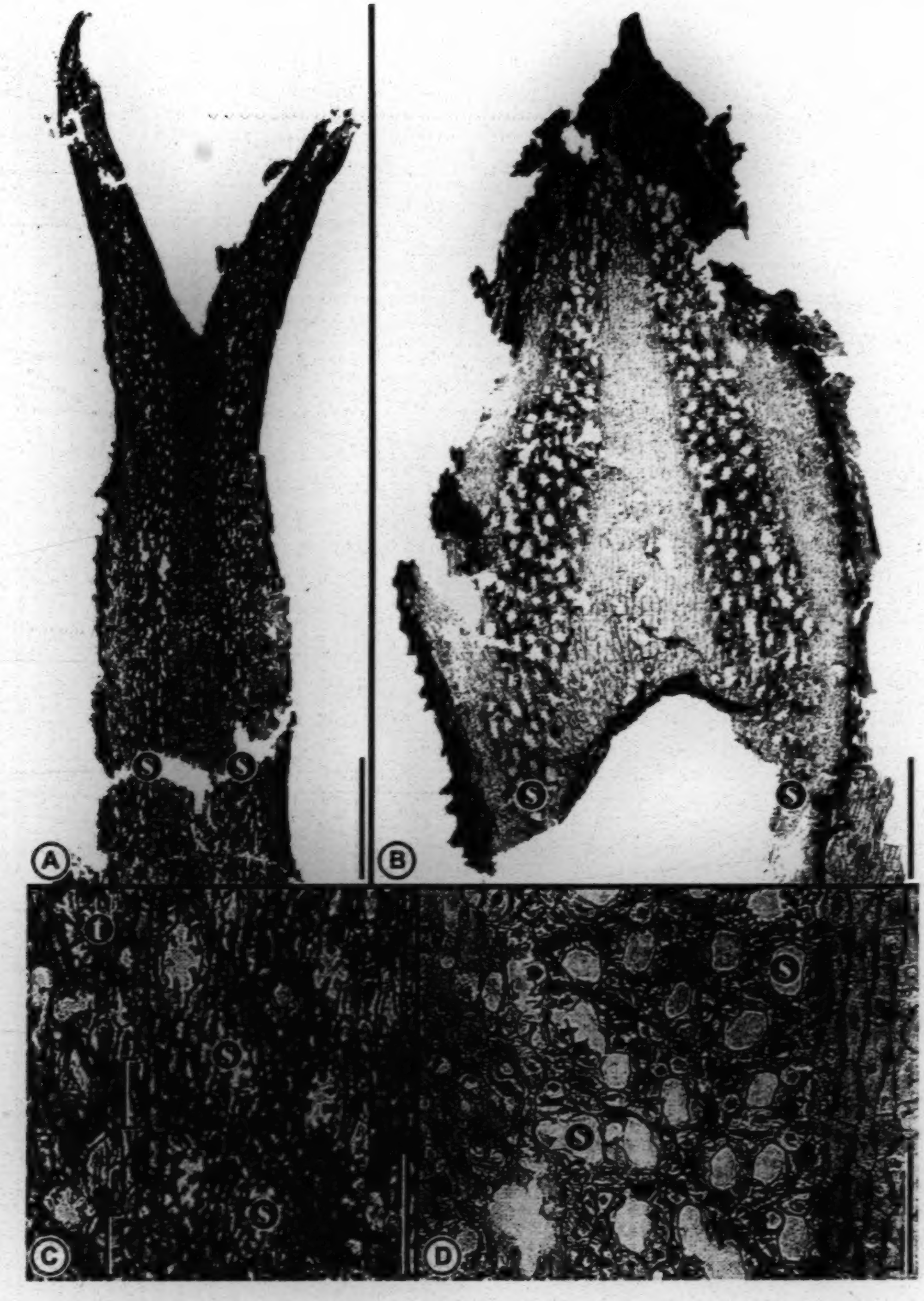
Figs. 5A-D. *Emporia royalii* sp. nov., cuticular macerations of leaves on penultimate and ultimate shoots. **A.** Adaxial surface of forked leaf on penultimate shoot showing two broad bands of stomata (s) separated by stomatal free zone. M 2986-7, scale bar = 0.5 mm. **B.** Adaxial surface of leaf of ultimate shoot showing subtriangular shape, two bands of stomata (s) and stomatal free zone. M 591-1, scale bar = 0.3 mm. **C.** Adaxial surface of leaf on penultimate shoot showing elongated epidermal cells (brackets) separating stomata (s) and circular trichome bases (t). M 2986-7, scale bar = 70 μm. **D.** Adaxial surface of leaf on ultimate shoot showing stomatal band (s) and papillate epidermal cells on both sides of the band. M 591-1, scale bar = 40 μm.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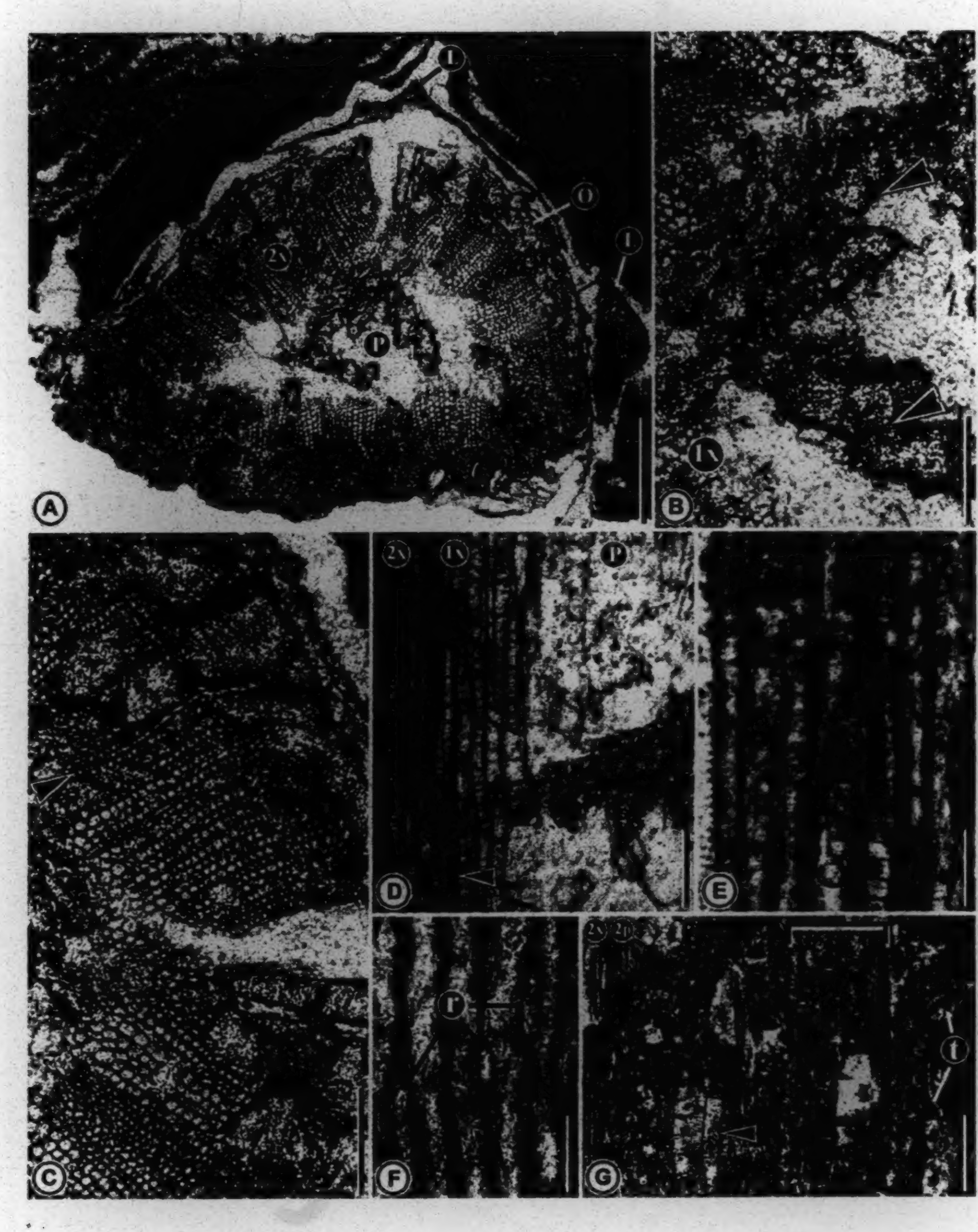
Figs. 6A-G. *Emporia royalii* sp. nov. anatomy of penultimate axis. **A.** Cross section showing pith with secretory cells (P), secondary xylem (2x), outer cortex (O), and leaves (l). M 1627-12, scale bar = 0.3 mm. **B.** Pith showing secretory cells (arrowheads). M 1627-12, scale bar = 0.5 mm. **C.** Cross section of secondary xylem showing tracheids and rays (arrowhead). M 1627-12, scale bar = 0.1 mm. **D.** Radial section showing secondary xylem (2x), primary xylem (1x) with helical thickenings on secondary walls (arrowhead), and pith (P) with sclerotic nest. M 1627-1, scale bar = 54 μm. **E.** Radial section showing metaxylem (on left) and secondary xylem tracheids with circular bordered pits (on right). M 1627-2, scale bar = 17 μm. **F.** Tangential section showing uniseriate rays (r). M 1627-2, scale bar = 15 μm. **G.** Longitudinal section showing secondary xylem (2x), secondary phloem area (2P), outer cortex with parenchyma cells and secretory cells (bracket), and epidermis with trichomes (t). M 1627-2, scale bar = 64 μm.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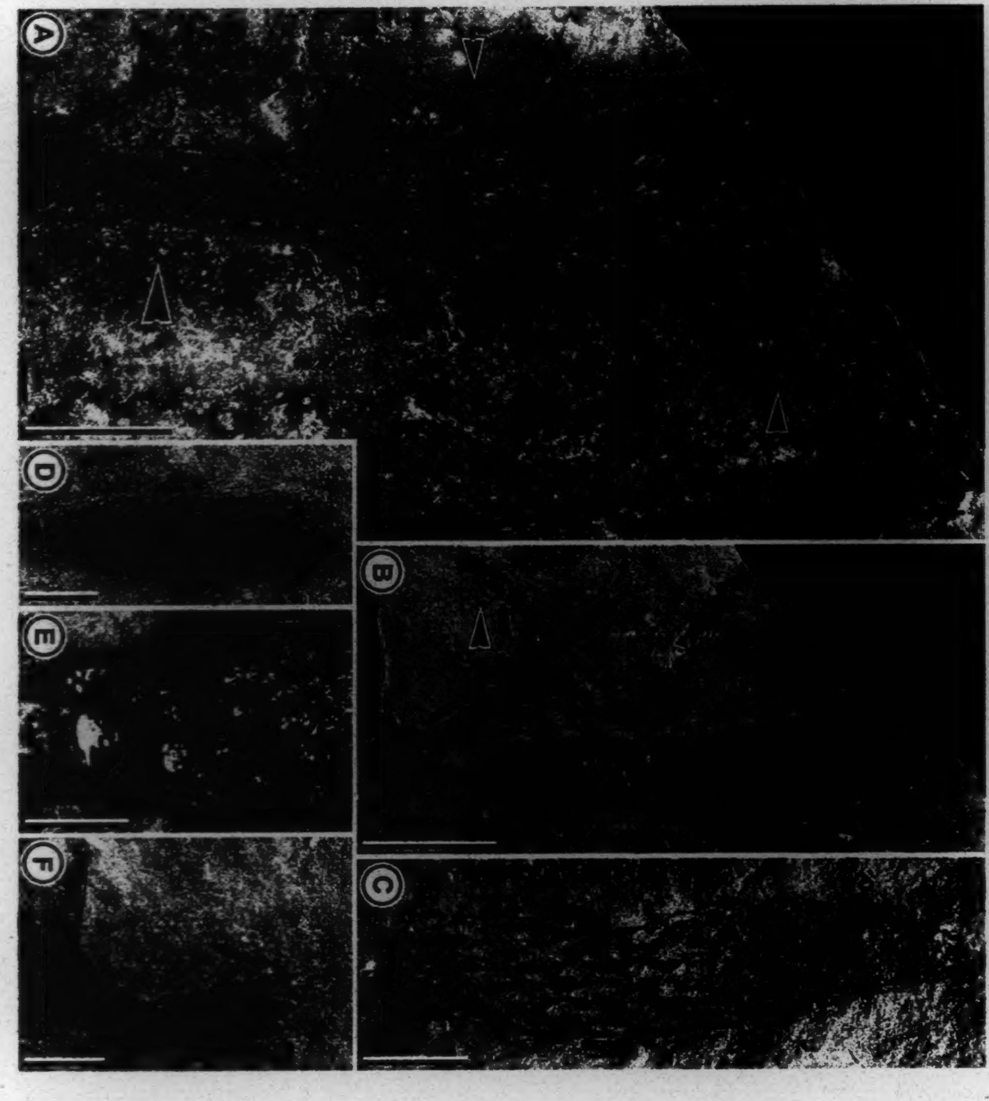
Figs. 7A-F. *Emporia cryptica* sp. nov., pollen cones. **A.** Lateral branch showing ultimate shoots with terminal simple pollen cones. Note leaves on penultimate (large arrowhead) and ultimate shoots (small arrowheads). M 3985 B, scale bar = 1 cm. **B.** Ellipsoidal cone attached to ultimate shoot. M 1617 B, scale bar = 1 cm. **C.** Mature ellipsoidal cone with helically arranged microsporophylls. M 4004, scale bar = 5 mm. **D.** Immature cone. M 591, scale bar = 5 mm. **E.** Immature pollen cone base showing microsporophylls and vegetative leaves at base. M 2962, scale bar = 3 mm. **F.** Immature cone attached to ultimate shoot. M 3099, scale bar = 5 mm.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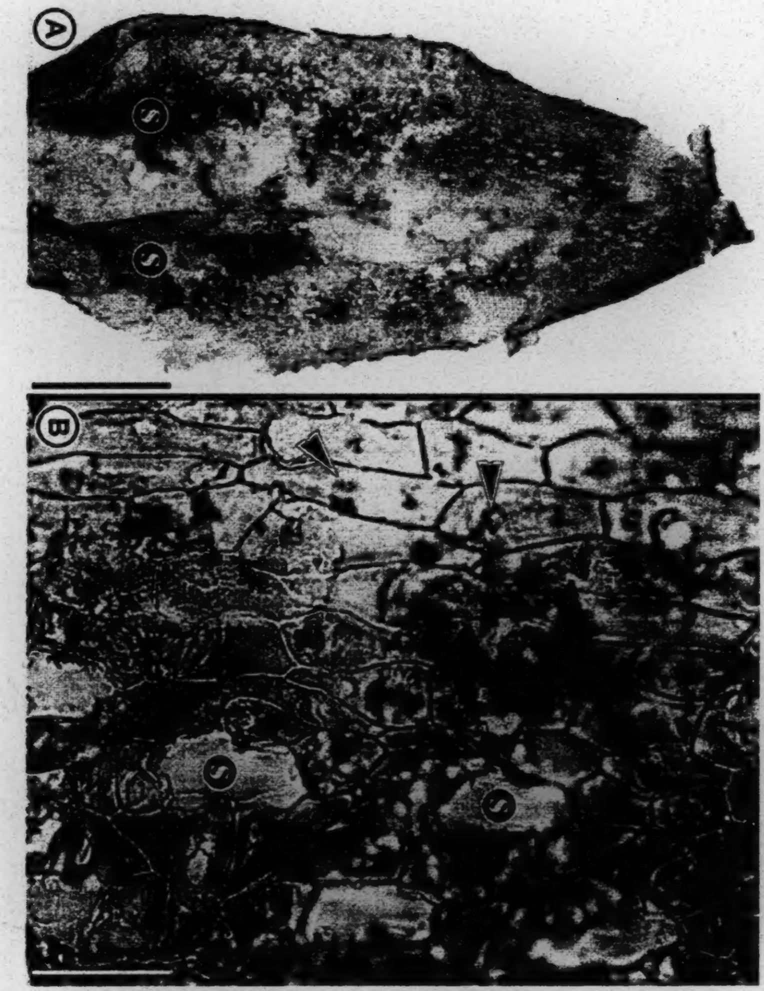
Figs. 8A-B. *Emporia royalii* sp. nov., leaves on ultimate shoot with attached pollen cone. **A**. Adaxial surface of subtriangular leaf from ultimate shoot with two bands of stomata (s). M 591-17, scale bar = 0.3 mm. **B**. Adaxial surface showing papillate epidermal cells (arrowheads) and stomata (s). M 591-17, scale bar = 0.02 mm.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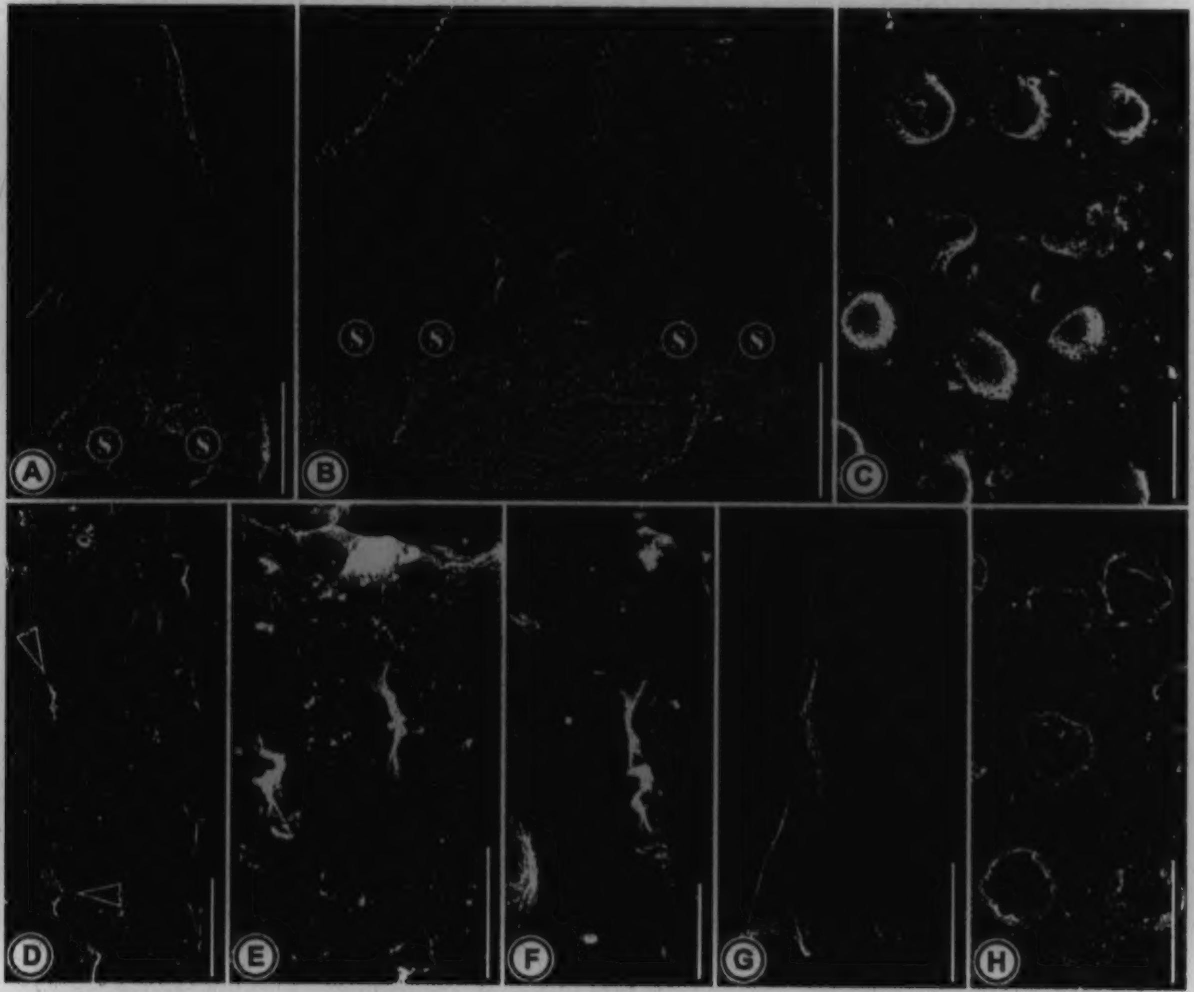
Figs. 9A-H. *Emporia royalii* sp. nov., SEM microsporophylls. All specimens macerated from M 2962. **A**. Narrowly triangular microsporophyll showing adaxial stomatal bands (s). Scale bar = 1 mm. **B**. Microsporophyll with two long and two short bands of stomata (s). Scale bar = 400 μm. **C**. Stomatal complex showing six subsidiary cells with erect and overarching papillae. Scale bar = 10 μm. **D**. Epidermal cells with normal papillae and undeveloped papillae (arrowheads). Scale bar = 20 μm. **E**. Adaxial undeveloped papillae. Scale bar = 10 μm. **F**. undeveloped papillae. Scale bar = 5 μm. **G**. Narrowly triangular microsporophyll showing abaxial surface. Scale bar = 1 mm. **H**. Abaxial trichome bases. Scale bar = 20 μm.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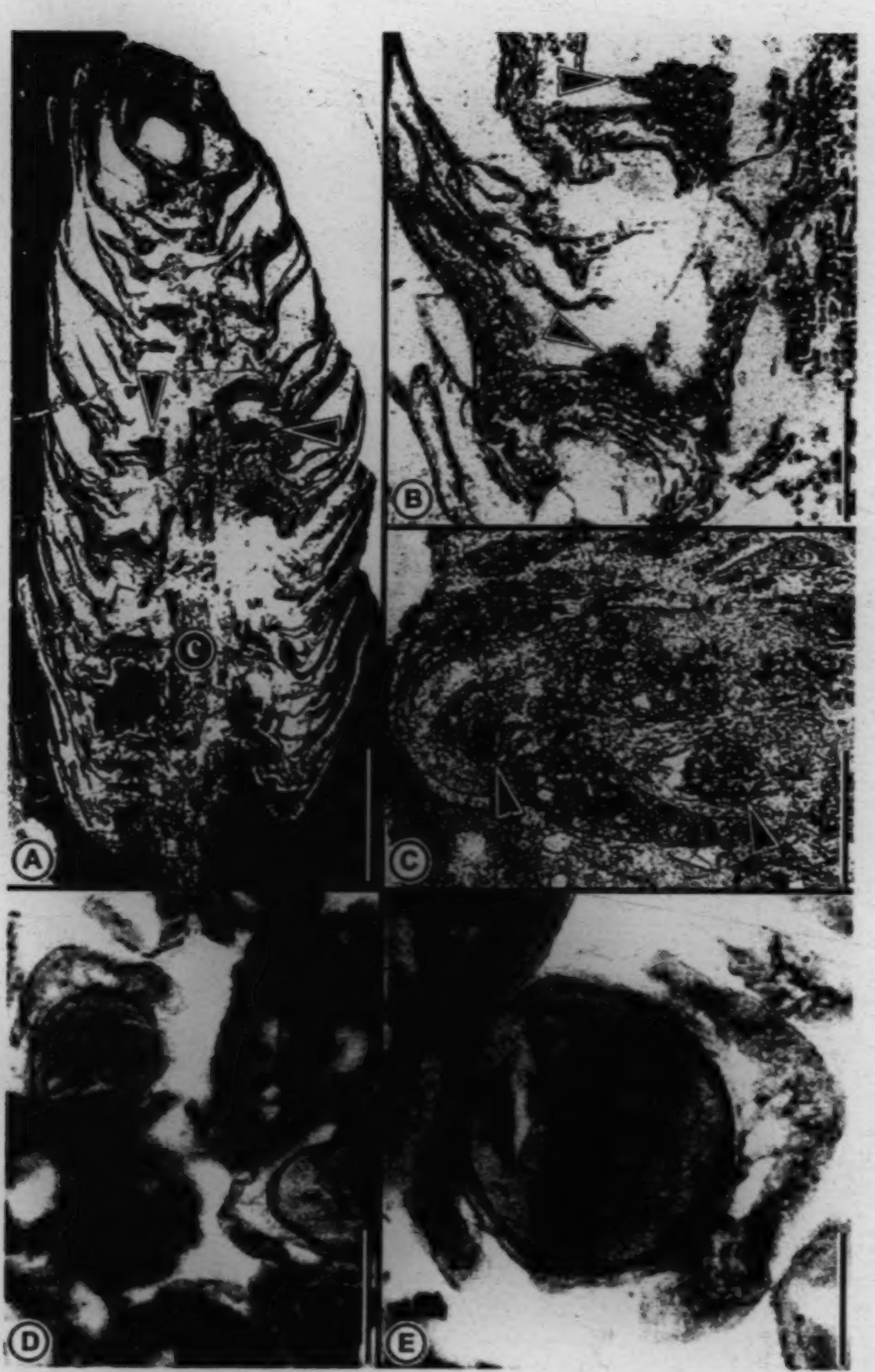
Figs. 10A-E. *Emporia royalii* sp. nov., anatomy of pollen cones. **A.** Longitudinal section showing cone axis (c), microsporophylls with pollen sac bases (arrowheads). M 1631-1, scale bar = 1.5 mm. **B.** Radial section showing microsporophylls with adaxial pollen sac bases on shanks (arrowheads). M 1631-1, scale bar = 700 μm. **C.** Cross section showing microsporophyll and pollen sacs with enclosed prepollen (arrowheads). M 80-2, scale bar = 300 μm. **D.** Monosaccate *Potonieisporites* prepollen grains in pollen sac. M 80-9, scale bar = 40 μm. **E.** Distal view of *Potonieisporites* grain showing saccus and corpus. M 80-9, scale bar = 18 μm.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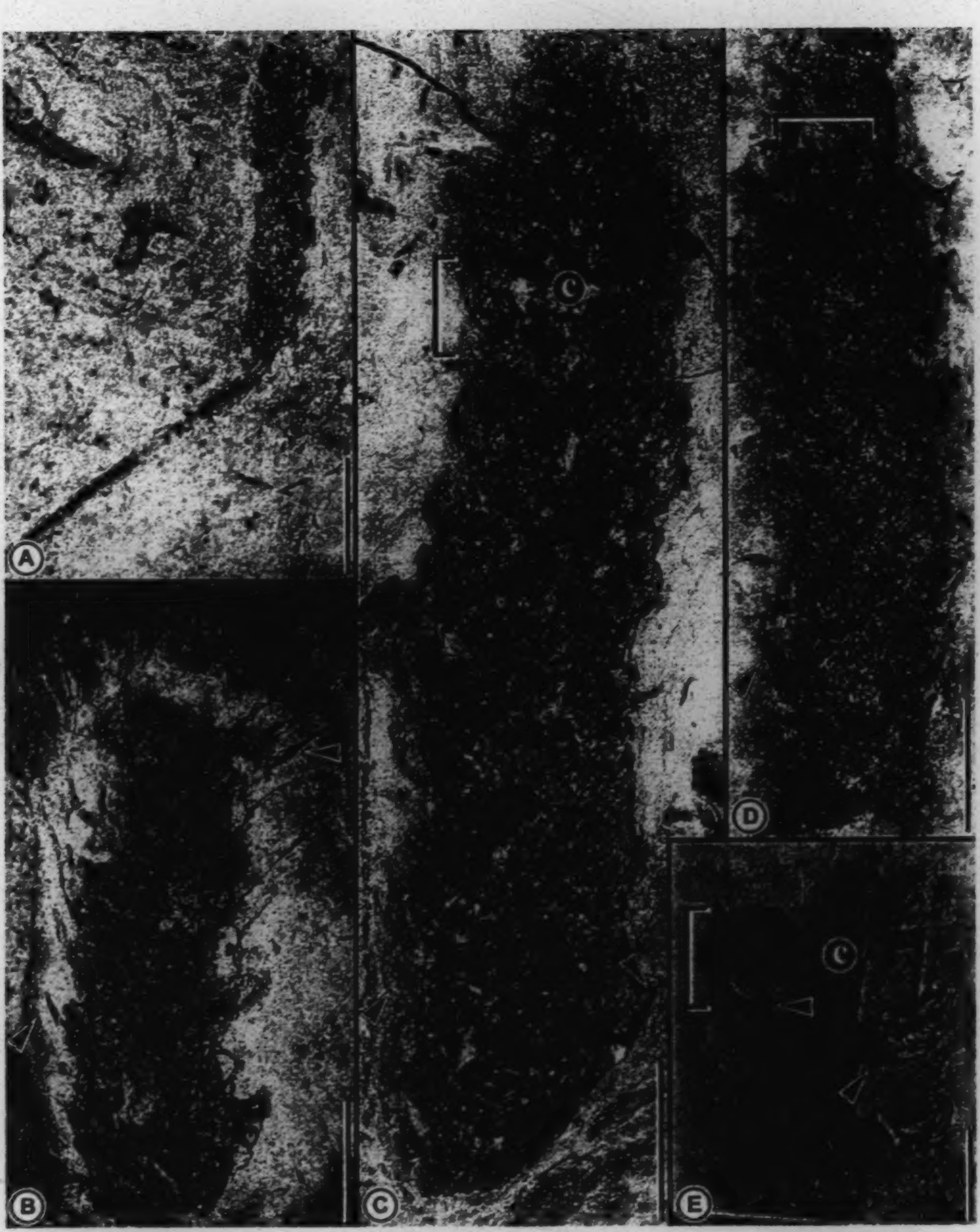
Figs. 11A-E. *Emporia royalii* sp. nov., ovulate cones. **A**. Cone attached to penultimate shoot. Holotype. M 2947 A, scale bar = 3 cm. **B**. Cone showing bract tips (arrowheads). M 1809, scale bar = 1 cm. **C**. Cone showing axis (c), bracts (black arrowhead), and axillary dwarf shoots (brackets). M 2969 B, scale bar = 1 cm. **D**. Cone showing bract (arrowhead) and sterile scales in face view (bracket). M 1883, scale bar = 1 cm. **E**. Longitudinal section showing axis (c), bracts (arrowheads), and axillary dwarf shoots (bracket). M 1662, scale bar = 5 mm.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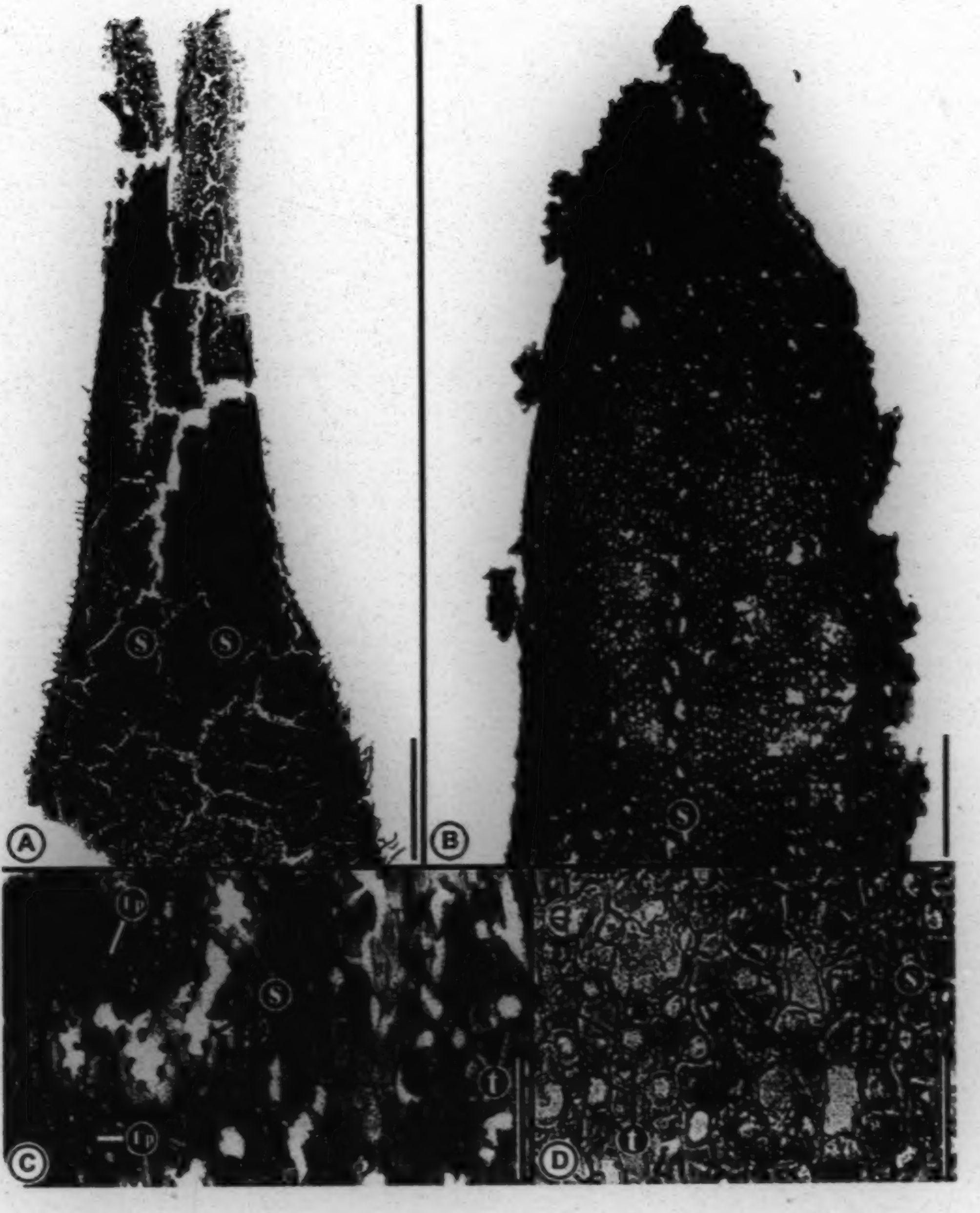
Figs. 12A-D. *Emporia royalii* sp. nov., cuticular macerations of bracts and sterile scales from ovulate cones. **A**. Adaxial surface of forked bract showing two stomatal bands (s). M 2986-10, scale bar = 1 mm. **B**. Abaxial surface of sterile scale showing narrow band of stomata (s). M 1613-8, scale bar = 200 μm. **C**. Abaxial surface of bract showing band of stomata (s) and thick-walled cells between stomata (Ep). M 2986-10, scale bar = 600 μm. **D**. Scale abaxial surface showing trichome bases (t), and narrow stomatal band (s). M 1613-Br1, scale bar = 45 μm.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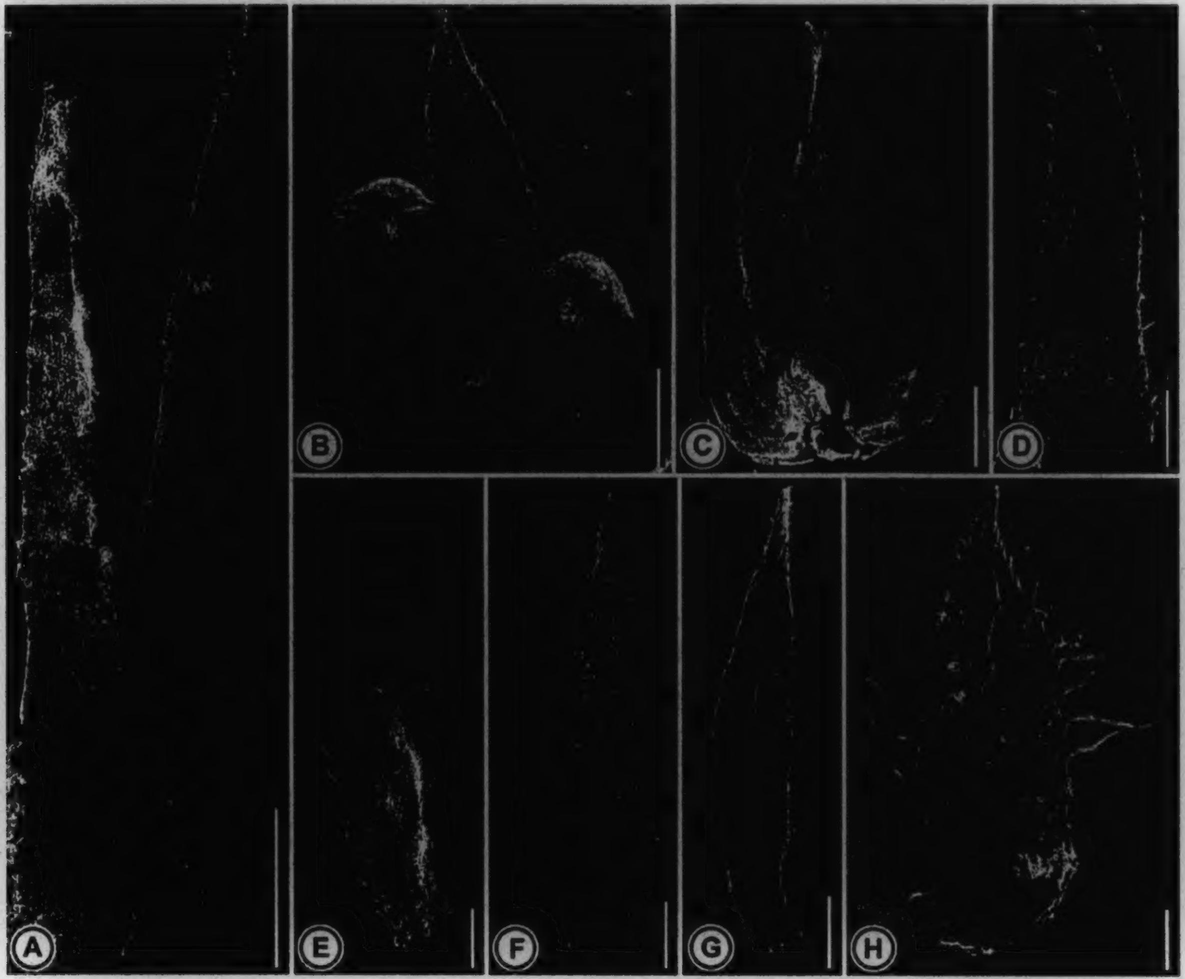
Figs. 13A-H. *Emporia royalii* sp. nov., SEM of bracts and sterile scales from ovulate cones. All specimens macerated from M 1883. **A.** Adaxial surface of forked bract showing stomata (s). Scale bar = 1 mm. **B.** Abaxial surface showing two sporophylls with seed scars and sterile scale. Scale bar = 1 mm. **C.** Abaxial surface of inflated bract. Scale bar = 1 mm. **D.** Triangular sterile scale with marginal trichomes. Scale bar = 0.5 mm. **E.** Abaxial surface showing two linear sterile scales with marginal trichomes. Scale bar =1 mm. **F.** Abaxial surface showing narrowly triangular shape and marginal trichomes. Scale bar = 1 mm. **G.** Adaxial surface showing narrowly lanceolate shape. Scale bar = 0.5 mm. **H.** Abaxial surface showing very large marginal trichomes. Scale bar = 0.2 mm.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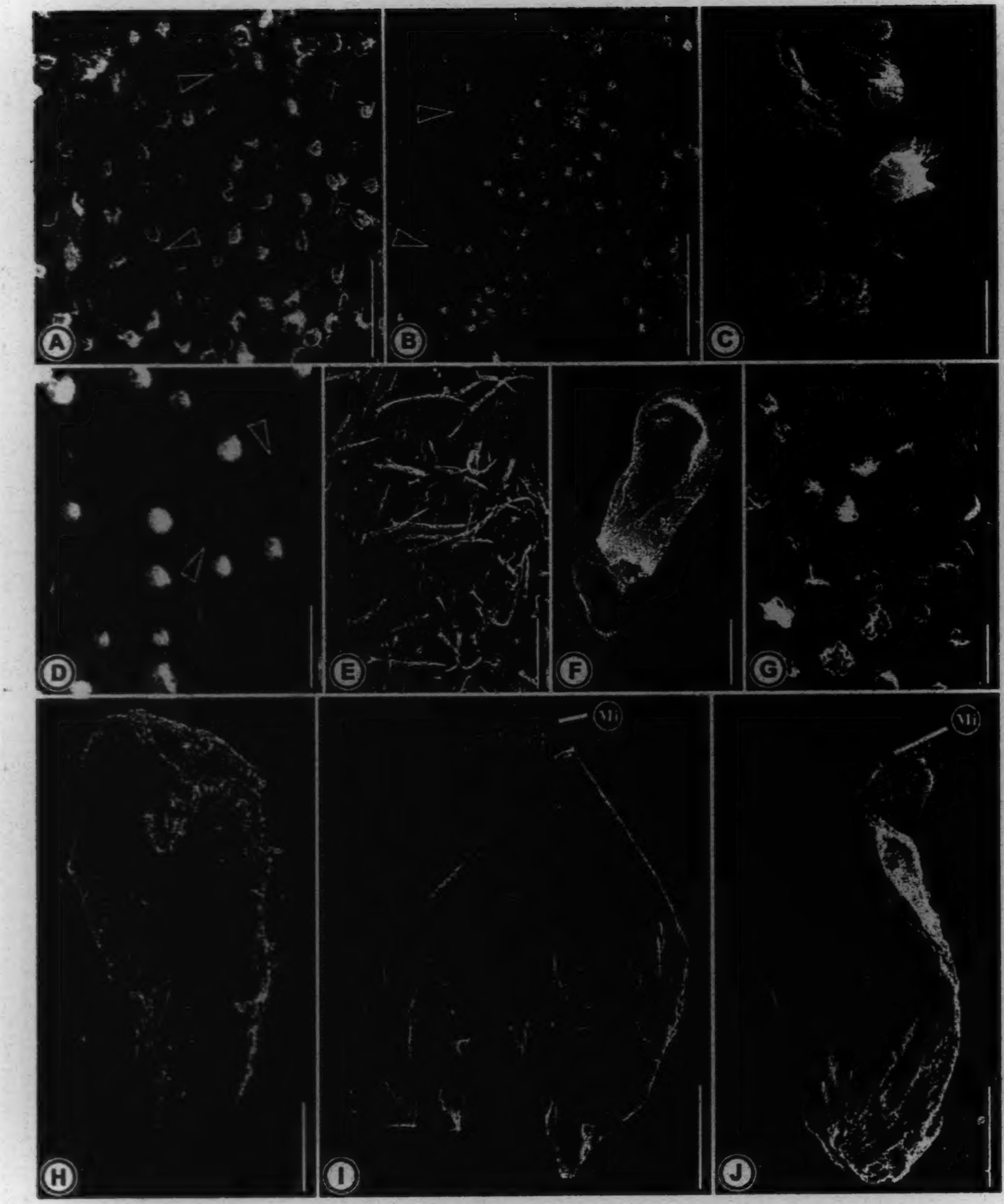
Figs. 14A-J. *Emporia royalii* sp. nov., SEM of cuticular features of bract, sterile scales, sporophyll, and seeds. All specimens macerated from M 1883, unless otherwise indicated. **A.** Bract showing adaxial stomata (arrowheads) with erect to overarching papillae. Scale bar = 50 μm. **B.** Bract showing adaxial narrow band of stomata, undeveloped papillae (arrowheads), and papillae. Scale bar = 100 μm. **C.** Adaxial surface of sterile scale showing stomatal complex with overarching papillae on subsidiary cells. Scale bar =10 μm. **D.** Adaxial surface of sterile scale showing erect papillae and undeveloped papillae (arrowheads). Scale = 500 μm. **E.** Sterile scale showing long and narrow trichomes. Scale bar = 100 μm. **F.** Sterile scale showing short and broad trichome. Scale bar = 20 μm. **G.** Sterile scale showing small abaxial trichome bases. Scale bar = 10 μm. **H.** Sporophyll showing sub-apical seed scar and small trichome bases. Scale bar = 500 μm. **I.** Seed with micropylar end (Mi). Scale bar = 100 μm. **J.** Seed showing micropyle (Mi). M 1662, scale bar = 500 μm.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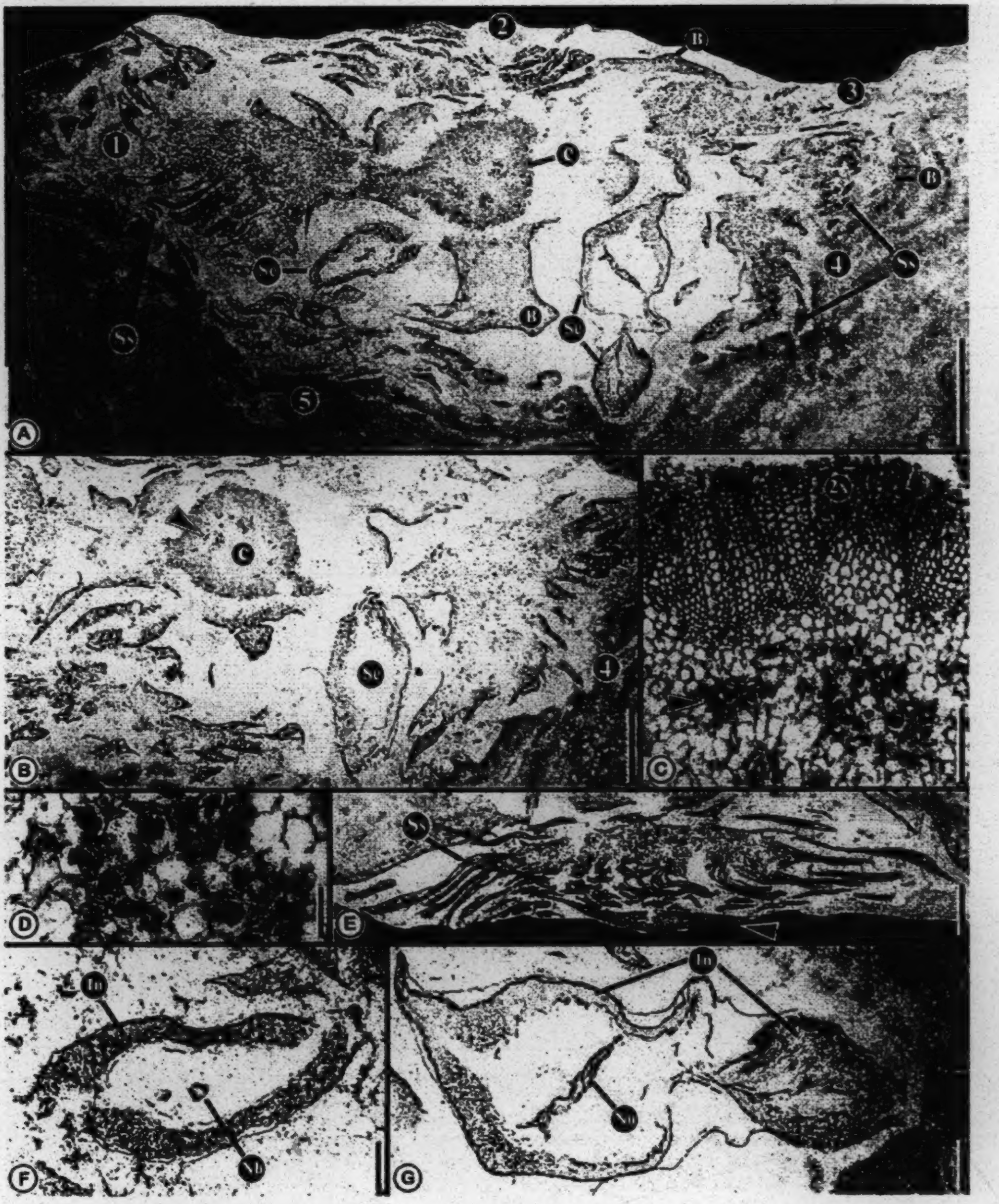
Figs. 15A-G. *Emporia royalii* sp. nov., ovulate cone anatomy. **A.** Cross section showing cone axis (c), axillary dwarf shoots (numbers) with sterile scales (Ss), and seeds (Se). M 2986 B-16, scale bar = 0.8 mm. **B.** Cross section showing cone axis (c) and axillary dwarf shoot (number 4) with seed (Se). M 2986 B-43, scale bar = 2 mm. **C.** Cone axis showing pith with secretory cells (arrowhead) and secondary xylem (2x). M 2986 B-24, scale bar = 0.3 mm. **D.** Cross section of sclerotic nest in pith. M 2986 B-44, scale bar = 5 μm. **E.** Cross section of axillary dwarf shoot showing subtending bract (arrowhead) and several sterile scales (Ss). M 2986 B-38, scale bar = 0.6 mm. **F.** Seed showing integuments (In) and nucellar beak (Nb). M 2986 B-24, scale bar = 0.4 mm. **G.** Seeds showing integuments (In) and collapsed nucellus (Nu). M 2986 B-35, scale bar = 0.45 mm.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CHAPTER 6

Phylogeny of walchian conifers

Introduction

Fossil conifers are usually preserved as isolated and often fragmentary plant organs that include lateral branches with leaves, pollen cones and ovulate cones (e.g., Florin 1927, 1938-45, 1950, 1951). However, taxa based on isolated and fragmentary specimens do not reflect the complete suite of characters present in a single reconstructed species (Kerp et al. 1990; Mapes and Rothwell 1991; Rothwell and Mapes 2001; Hernandez-Castillo et al. 2001b; chapters 3-5 in this dissertation) and they cannot be used to infer phylogenetic relationships. Therefore, isolated conifer remains have to be unequivocally correlated in order to produced accurate whole plant reconstructions. This process requires large numbers of specimens identified by means of morphological, cuticular, and anatomical characters and organic connections (Rothwell and Mapes 2001; Hernandez-Castillo et al. 2001b; chapters 3-5 in this dissertation). Whole plants are essential to understand characters, character states, diagnostic characters, and possible synapomorphies among fossil conifers. In spite of this, the use of whole plants in systematic studies of fossil conifers is relatively new (Clement-Westerhof, 1984, 1987; Kerp et al. 1990; Mapes and Rothwell 1991; Rothwell and Mapes 2001; Hernandez-Castillo et al. 2001b; chapters 3-5 in this dissertation).

The systematics of Paleozoic conifers was initially studied by Florin (1927, 1938-45, 1951) and his concepts stood unchallenged until more recent studies started to question these interpretations of the most primitive conifers (i.e., Schweitzer 1963; Rothwell 1982; Clement-Westerhof 1984, 1987; Mapes and Rothwell 1984; Mapes and Rothwell 1991, 1998; Kerp et. al. 1990; Hernandez-Castillo et al. 2001b, 2003; Rothwell and Mapes 2001). New studies have proposed two widely used classifications (Visscher et al. 1986;

Mapes and Rothwell 1991) and the description of new taxa worldwide (i.e., Winston 1984; Kerp and Clement-Westerhof 1991; Galtier et al. 1992; Broutin and Kerp 1994; Freytet et al. 1996; Kerp et al. 1996; Meyen 1997; Lausberg and Kerp 2000; Lausberg 2002; Mapes and Rothwell 2003; Rothwell et al. 2005). However, most of these taxa have not been fully reconstructed and only a few of them are known as complete plants (Clement-Westerhof 1984, 1987; Cuneo 1985; Archangelsky and Cuneo 1987; Kerp et al. 1990; Meyen 1997; Barthel and Noll 1999; Rothwell and Mapes 2001; Hernandez-Castillo et al. 2001b; Rothwell et al. 2005; chapters 3-5 in this dissertation).

Phylogenetic relationships among conifers have been assessed at different taxonomic levels using both morphological (Eckenwalder 1976; Hart 1987; Miller 1999) and molecular analyses (Wang and Szmidt 1993; Brunsfeld et al. 1994; Price et al. 1998; Setoguchi et al. 1998; Stefanovic et al. 1998; Shindo et al. 1999; Winter et al. 1999; Liston et al. 1999; Bowe et al. 2000; Chaw et al. 2000; Gadek et al. 2000; Kusumi et al. 2000; Gernandt et al. 2003, 2005). Some analyses have resolved living conifers as monophyletic (Crane 1985; Doyle 1996; Magallón and Sanderson 2004; Rydin et al. 2002) or paraphyletic with Gnetales placed within conifers (gnepine hypothesis: Bowe et al. 2000; Donoghue and Doyle 2000; Soltis et al. 2002; Burleigh and Mathews 2004). However, few analyses include fossil conifers and most of these deal with seed plant phylogeny as a whole rather than conifer phylogeny per se (Crane 1985; Nixon et al. 1994; Rothwell and Serbet 1994; Doyle and Donoghue 1986; Donoghue and Doyle 2000; Magallón and Sanderson 2002; Soltis et al. 2002; Burleigh and Mathews 2004).

Only two analyses have focused on conifer phylogeny including fossil taxa (Miller 1999; Rothwell et al. 2005). Miller (1999) analyzed phylogenetic relationships among extinct and extant conifers based on a small set of characters from ovulate cones and proposed several scenarios for the evolution of modern groups. However, his analysis was based on morphotaxa that do not reflect complete plants (Hernandez-Castillo et al. 2001b). Rothwell et al. (2005) assessed phylogenetic relationships using complete or nearly complete fossil taxa, providing a preliminary phylogeny for the most ancient conifers. This paper includes the second phylogenetic analysis of the most primitive conifers that include whole plants. It discusses phylogeny, current systematics, and possible synapomorphies among Paleozoic conifers.

Materials and Methods

Taxon Sampling. Twenty four whole plant species of the most ancient conifers and coniferophytes (Table 1) and fifty seven characters (Appendix 1) were included in the analysis. The character matrix used (Appendix 2) was modified from Rothwell et al. (2005). Taxa include nine species of late Pennsylvanian and early Permian walchian conifers from Europe and North America, three conifers from the early to middle Permian of Russia (Angara), two from the middle Permian of Argentina (Gondwana), five species from the late Permian and one from the middle Triassic of Europe. Other taxa included two conifer-like plants from the late Pennsylvanian-early Permian of North America and Europe. The analysis also includes two species of Cordaitales from the late Pennsylvanian of North America and a late Pennsylvanian seed fern as the outgroup (Table 1).

Phylogenetic Analysis. Phylogenies were reconstructed using equal weighted maximum parsimony (heuristic search; PAUP, version 4.0b2, Swofford 2003) and parsimony and ratchet-based searches in NONA, version 2.0 (Goloboff 1999) implemented in WinClada (version 1.00.08, Nixon 2002). To increase the probability that the most parsimonious trees would be found, analyses were replicated 1,000 times using the random addition sequence option. To minimize *a priori* assumptions about the relative value of characters, all characters were unweighted and unpolarized, and multistate characters were unordered. Branch support was estimated with the boot strap and jackknife options of PAUP (full heuristic search, 1000 replicates each) and WinClada, (1000 replicates each), and decay analysis. Equally parsimonious trees from all analyses were summarized using strict consensus.

Character mapping. Character and character states were mapped and reconstructed using MacClade 4.03 (Maddison and Maddison 2001) and WinClada. All characters were mapped on the strict consensus tree of the two most parsimonious trees retrieved using parsimony and ratchet searches. Character exclusion was done using the most informative characters on each node of the strict consensus tree. Characters were excluded systematically until a shortest tree was found and all nodes on the trees were resolved. Characters 6, 10, 12, 15, 16, 32, 33, 52, and 53 were excluded one at a time, in pairs of characters (10-12, 10-15, 10-16, 12-15, 12-16, 15-16), sets (set 1: 10, 12, 15, 16; set 2: 6, 32, 33, 52, 53), and all characters at the same time. A third set of analyses involved the exclusion of the following taxa: *Concholepis harrisii, Timanostrobus muravievii* and *Kungurodendron sharovii*, *Genoites patagonica*, *Ernestiodendron filiciforme*, *Thucydia mahoningensis*, *Voltzia hexagona*, *Aetophyllum stipulare*, *Dolomitia cittertiae*, *Hanskerpia hamiltonensis*, *Barthelia furcata*, and *Otovicia hypnoides*. All exclusion analyses were performed using the same tree search and branch support options as the initial analysis.

Results

Phylogenetic relationships of all 23 taxa were resolved using the Late Pennsylvanian seed fern *Callistophyton poroxyloides* as the outgroup. Results were identical using both parsimony and ratchet analyses using PAUP and NONA respectively. Two most parsimonious trees of 183 steps (ratchet, CI=0.46; RI=0.62) and 185 (parsimony, CI=0.46; RI=0.62) were obtained. One thousand random addition replicates for both parsimony and ratchet searches yielded the same two most parsimonious trees of 183 and 185 steps. A strict consensus tree of the two most parsimonious trees produced identical topologies in all analyses (Fig. 1). Bootstrap and jacknife percentages (with 40% replacement) are low for many nodes throughout the tree (Fig. 1). Bootstrap values above 50% are recorded above the relevant branches on the tree and jacknife values above 50% are recorded below the branches (Fig. 1). Decay analyses yielded 48 trees at 186 steps or less, 605 trees at 187 steps or less, and 5,780 trees of 188 steps or less; these decay values are placed to the left of the relevant branches on the tree (Fig. 1).

The strict consensus tree (Fig. 1) shows the cordaiteans (*Cordaixylon dumusum* + *Mesoxylon priapii*) at the base of the tree, with the Vojnovskyean plant and Dicranophyllum *hallei* attached at successively higher nodes. The tree resolves all primitive conifers (Voltziales) as a clade, sister to *D. hallei*. The next node on the tree is a polytomy that includes the angaran Voltziales (*Concholepis harrisii, Timanostrobus muravievii* and *Kungurodendron sharovii*), a Gondwana Voltziales clade (*Feruglioocladus* spp. + *Genoites patagonica*), and a clade containing the remaining Walchian, Voltzian and lebachioid taxa. This remaining walchian Voltziales clade has *Thucydia mahoningensis* at its basal split, followed by *Ernestiodendron filiciforme* at the next higher node followed by a node with a Voltzian and Lebachioid clade. The voltzian Voltziales clade includes (*Ortiseia* spp. + (*Voltzia hexagona* + (*Aethophyllum stipulare* + (*Dolomitia cittertiae* + *Majonica alpina*))); the Lebachioid clade includes a basal polytomy of *Hanskerpia hamiltonensis* and *Barthelia furcata*, *Otovicia hypnoides* + *Utrechtia floriniformis*, and the Emporiaceae (*Emporia lockardii* (*Emporia cryptica* + *Emporia royalii*).

Bootstrap and jacknife analyses only show support values above 50% for the cordaitalean clade, Vojnovskyean plant, Voltziales, Gondwanan clade, the voltzian Voltziales, as well as the Emporiaceae within the Lebachioid clade (Fig. 1). Characters mapped on the strict consensus tree show characters and character states that support each node on the tree (Fig. 2). Individual characters were analyzed and systematically chosen for exclusion in subsequent analyses as outlined in methods. Length of the shortest tree decreased every time certain characters were excluded from the initial trees (L=183, and 185 steps). Nine characters (6, 10, 12, 15, 16, 32, 33, 52 and 53) were eventually removed producing a shortest tree of 141 steps for both ratchet and parsimony (CI= 50; RI=67).

The shortest tree topologies were consistent when more than three characters were excluded in parsimony and ratchet searches (Fig. 3). When all nine characters were excluded from the analysis, the shortest tree has *D. hallei* at the very base the Voltzian conifers. The next node shows two main clades, with the first clade including *T. muravievii* as sister to the Gondwanan Voltziales, and the second clade with the remaining voltzialean conifers. The base of this second clade shows a grade that includes *C. harrisii*, *K. sharovii*, *T. mahoningensis*, and *E. filiciforme* followed by the Voltzian and Lebachioid distal clades. The voltzian Voltziales clade has *Ortiseia* at the base followed by *V.*

hexagona, and a distal clade containing *A. stipulare* + (*D. cittertiae* + *M. alpina*). The Lebachioid clade is fully resolved and renders *U. floriniformis* at the base followed by *O. hypnoides* as sister to two terminal clades, ((*B. furcata* + *H. hamiltonensis*) + the Emporiaceae). Further 1000 random addition replicates for all analyses generated the same tree. However, bootstrap and jacknife percentages were low for most nodes throughout the tree (Fig. 3).

Discussion

Results of these phylogenetic analyses support some of the previous hypotheses of relationships among Paleozoic coniferophytes and conifers. This study, like that of Rothwell et al. (2005), resolves a single clade that includes all voltzialean conifers, and within the Voltziales there are three fully resolved clades (Gondwanan, Voltzian and Lebachioid Voltziales). However, these results do not support the current circumscription for the Utrechtiaceae Rothwell and Mapes (=Walchiaceae sensu Clement-Westerhof) and question the previous placement of *Hanskerpia* within the Emporiaceae (Mapes and Rothwell 2003; chapter 3 in this dissertation), as well as its relationship to the Bartheliaceae (Rothwell and Mapes 2001).

The strict consensus tree (using of all characters) shows a similar topology to that presented by Rothwell et al. (2005). However, an important difference is the inverse position of the two most distal clades (Lebachioid and Voltzian) on the tree (Fig. 1; Rothwell et al. 2005, Fig. 10). In both analyses, the Late Pennsylvannian cordaitaleans and the late Pennsylvannian to early Permian Vojnovskyean plant are resolved as successively more closely related sister groups to the primitive conifers of the Voltziales

(Figs. 1-4; Fig. 10, Rothwell et al. 2005). Our results reinforce the position of *Dicranophyllum* (early Permian) on the tree, but this taxon may be a basal conifer or the sister group to the Order Voltziales, contrasting with the Rothwell et al. (2005) analysis, in which *Dicranophyllum* was considered a basal conifer and not as the sister group to the conifers due to the high jacknife support and decay values.

The Gondwanan clade (*G. patagonica* + *Feruglioclaclus* spp.) is well supported providing evidence of a basal group of conifers in South America. However, this clade is part of a basal polytomy that includes all Angaran (*C. harrisii*, *T. muravievii*, and *K. sharovii*), and the Euramerican conifers as previously observed by Rothwell et al. (2005). Alternative topologies when characters are excluded from our analysis show that *T. muravievii* may be more closely related to taxa within the Gondwanan clade, but there was no bootstrap or jacknife support for this relationship.

The next successive nodes on the tree are defined by *T. mahoningensis* and *E. filiciforme*, which are located at the base of the Voltzian and Lebachioid clades as in Rothwell et al. (2005), indicating that these taxa are sister to the Voltzian and Lebachioid Voltziales clades. *Thucydia mahoningensis* was described as the type species of the monotypic family Thucydiaceae and is unique in having compound pollen cones and compound fertile zones (Hernandez-Castillo et al. 2001a, 2001b). *Ernestiodendron filiciforme* has been considered as a typical Utrechtiaceae Rothwell and Mapes (=Walchiaceae sensu Clement-Westerhof) walchian conifer (Florin 1938-45; Kerp et al. 1990; Mapes and Rothwell 1991; Hernandez-Castillo et al 2001b). Nevertheless, its position on the tree does not include it in either the Lebachioid or Voltzian clades suggesting that this species does not belong to the Utrechtiaceae (=Walchiaceae) as previously proposed (Visscher et al. 1986; Mapes and Rothwell 1991; Lausberg and Kerp 2000).

The most distal clades on the tree are the Voltzian and the Lebachioid Voltziales. The Voltzian clade, composed of five European walchian conifers, that have been placed within three different families of Voltzialean conifers: the Utrechtiaceae (=Walchiaceae), the Majonicaceae, and the Aethophyllaceae (Table 2; Grauvogel-Stamm 1978; Visscher et al 1986; Clement-Westerhof 1987; Mapes and Rothwell 1991; Rothwell and Mapes 2003). Our analyses do not support current familial circumscription of Utrechtiaceae (=Walchiaceae), and a relationship with the upper Permian Majonicaceae and the middle Triassic conifer *A. stipulare* is suggested.

The Lebachioid Voltziales are resolved as a distinct clade in all our analyses, supporting a Late Pennsylvanian Lebachioid clade (Mapes and Rothwell 1991). Rothwell et al. (2005) previously designated this group as a paraphyletic assemblage within the walchian Voltziales that include *Ernestiodendron filiciforme* + (*Thucydia mahoningensis* + Lebachioid clade). Taxa included in the Lebachiod clade in our analyses have been placed in Utrechtiaceae (=Walchiaceae) (*U. floriniformis, O. hypnoides*), the Bartheliaceae (*B. furcata, H. hamiltonensis*), and the Emporiaceae (*E. lockardii, E. cryptica,* and *E. royalii*). However, exclusion of characters 10, 12, 15 and 16 in our analysis suggests that *U. floriniformis* and *O. hypnoides* are basal to the clade that includes *B. furcata* + *H. hamiltonensis* and the Emporiaceae. This may indicate that *Barthelia* and *Hanskerpia* are more closely related, and part of a late Pennsylvanian clade that is sister to Emporiaceae. The analysis questions the original placement of *Hanskerpia* in the Emporiaceae (Rothwell et al. 2005), and the relative position of the early Permian conifers *U. floriniformis* and *O.*

hypnoides. My analysis also adds more controversy to the delimitation of the family Utrechtiaceae (=Walchiaceae), and the family delimitation needs to be emended.

Character mapping. The Voltziales clade is defined by characters: 8 (vegetative leaf shape), 12 (leaf cushions or consistently shaped leaf scars), 16 (adaxial stomata), and 18 (subsidiary cell positions) (Fig. 2; Appendix 1). When characters 12 (leaf cushions or consistently shaped leaf scars) and 16 (adaxial stomata) are removed, the basal polytomy in the Voltziales clade is resolved showing a basal clade (*Timanostrobus* + (*G. patagonica* + *F.* spp.) followed by the rest of the Angaran and Euramerican conifers (Fig 3). The *Timanostrobus* + Gondwanan clade is characterized by scattered abaxial stomata (character 18), while the Gondwanan clade is supported by a single terminal ovule borne on axillary dwarf shoots that lack distinct sporophylls and sterile scales (characters 34, 44, 46, 49 and 50, Appendix 1). The rest of the Voltziales are characterized by bilaterally symmetrical axillary dwarf shoots (character 43), and ovules produced either adaxially, laterally, or terminally (character 44).

The strict consensus tree when all characters are included shows a distal clade that includes *Thucydia*, *Ernestiodendron* and the Voltzian-Lebachioid clade. This clade is supported by orthotropic stems (character 1), plagiotropic lateral branches (character 2), subsidiary cells with prominent papillae (character 20), surficial trichomes (character 21), inverted ovules (character 45) and less than eight ovules per axillary dwarf shoot (character 49), and comprises the most ancient Euramerican conifers.

Thucydia is found at the base of the Euramerican conifers and can be differentiated from all other Euramerican conifers by a combination of characters that include compound pollen cones and compound fertile zones. *Ernestiodendron* plus the Voltzian-Lebachioid clade is supported by two synapomorphies: abaxial stomata (character 17) and simple pollen cones with peltate microsporophylls (26). Synapomorphies between the Voltzian and Lebachioid clades include reduced number of ovules (up to four, character 49) and apically aggregated sporophylls of the axillary dwarf shoot (character 54). When all characters are used in the analyses, the voltzian Voltziales clade is supported by three characters (46-48), but only two of them seem to be true synapomorphies ovules on visible sporophylls (character 46) and fused sporophylls producing fertile scales (character 47) when all nodes on the tree are resolved. The Lebachioid Voltziales clade is supported by five characters (4, 13, 35, 40, and 41, Appendix 1) when the base of the clade is a polytomy. However, when the clade is resolved, only two synapomorphies dissimilar penultimate and ultimate shoots (character 4) and the presence of forked bracts on ovulate cones (character 40) support this clade.

Even though a few synapomorphies can be found among the different clades, no clear synapomorphies between ancient and living conifers are apparent. Ancient conifers have leaves that are simple, narrow and needle-like, but these are plesiomorphies among recent fossil and extant conifers (Pilger 1926; Buchholz 1934; Chamberlain 1935; Taylor and Taylor 1993; Stewart and Rothwell 1993). Simple pollen cones are typical for both extinct and extant conifers but compound pollen cones are known in at least one ancient conifer (Hernandez-Castillo et al. 2001a). Some extant and fossil conifers have been interpreted as having compound pollen cones (Wilde 1944, 1975; Kerp et al. 1990; Assoumi 1994; Grauvogel-Stamm and Galtier 1998; Diez-Ferrer 2000), but evidence for these cones is equivocal (Mapes and Rothwell 1998; Hernandez-Castillo et al 2001a). This distinctness may indicate that *Thucydia* is a unique lineage at the base of the

Euramerican conifers.

The presence of compound ovulate cones is traditionally used as a synapomorphy for conifers (Pilger 1926; Chamberlain 1935), however, a few taxa in different parts of the tree (i.e., *Dicranophyllum*, *Thucydia*, *Voltzia*, and *Barthelia*) possess fertile zones instead of terminal cones. Clearly, no recognized synapomorphies defining both fossil and extant species are known, reinforcing previous analyses where the phylogenetic status of conifers (and coniferophytes) remains unresolved (e.g., Crane 1985; Nixon et al. 1994; Rothwell and Serbet 1994; Rothwell et al. 1997). We simply do not yet know if fossil and extant conifers are a monophyletic group. A larger number of whole plant reconstructions of Paleozoic, Mesozoic, and Cenozoic conifers will be needed to resolve this problem. Future phylogenetic analyses that include both whole plants and extant conifers will definitely help, because analyses restricted only to fossil or extant conifers will not be able to define relationships among all conifers.

Systematics of Primitive Conifers. Current classifications of primitive conifers differ in their approach in dealing with fossil conifer remains (Table 2; Visscher et al. 1986; Mapes and Rothwell 1991; Hernandez-Castillo et al. 2001b). The first classification scheme was proposed by Visscher et al. (1986) and relies on the promotion of species. The promotion of species allows conifer remains to be "promoted" to successively higher taxonomic hierarchies by adding newly discovered characters to the existing species. This system allows for different "stages" of knowledge for the specimens in question and helps to build a better concept for a particular species by adding more sets of characters over time (Visscher et al. 1986). These species, however, rely on fragmentary and/or isolated remains that may not reflect a whole plant (see Mapes and Rothwell 1991; Hernandez-

Castillo et al. 2001b), and lead to a subsequent proliferation of names (e.g., from *Lebachia* → *Hermitia* → *Culmitzchia* → *Walchia*) potentially increasing taxonomic confusion (Mapes and Rothwell 1991; Hernandez-Castillo et al. 2001b).

The second classification scheme was proposed by Mapes and Rothwell (1991) and relies on the reconstruction of fossil conifers as complete plants. This approach relies on clear correlations of fragmentary conifer organs that are based on several specimens of lateral branches, pollen cones, and ovulate cones (Hernandez-Castillo et al. 2001b; Rothwell and Mapes 2001; Rothwell et al. 2005; chapter 3-5 in this dissertation). Resulting species do not require of a proliferation of names and thus a more stable classification is maintained.

Such reconstructions are better used to assess systematic relationships among fossil conifers because they reflect whole plants (Rothwell et al. 2005). Whole plants allow us to assess and score ranges of variation within different vegetative and fertile organs. Understanding ranges of variation in a species is imperative because fossil conifers typically have overlapping sets of characters among species, making identification difficult (Hernandez-Castillo et al. 2001b; chapters 3-5 in this dissertation). Therefore, current classifications should reflect diagnostic characters of complete plants rather than isolated conifer remains.

Morphological characters for each ancient conifer family need to be reexamined and families emended (e.g., Emporiaceae, chapter 3 in this dissertation). Based on our analyses, the family Utrechtiaceae (= Walchiaceae sensu Clement-Westerhof) includes genera that are found in two completely different clades within the Voltizan Voltziales (*Ortiseia*) and the Lebachioid Voltziales (*Otovicia* + *Utrechtia*). Detailed reexamination of more European and North American taxa is urgently needed to test our present hypotheses of their relationships. Before proposing any formal taxonomic changes, to the already conflicting classifications, more fossil conifers need to be reconstructed to have a better understanding of the ranges of variation among known families. Based on our analyses and newly reconstructed conifers from the Hamilton Quarry (chapters 2-5 in this dissertation), characters that require further analysis include leaf morphology on different orders of branching, cuticular features of all leaves and leaf-like organs, pollen sac position, ovulate cone architecture and position, axillary dwarf shoot organization, and sporophyll number and position.

Future Phylogenetic Studies. Recently there has been renewed interest in the use of fossil taxa stemming from the development of new techniques that attempt to estimate divergence times and rates of evolution from molecular phylogenies (Sanderson 1998; Sanderson and Magallón 2002; Schneider et al. 2004; Magallón 2004). These techniques attempt to calibrate molecular phylogenies with paleontological data and serve as benchmark studies to improve our understanding of the relationships of modern groups and their most probable times of origin and/or divergence (Magallón 2004). However, the use of fossils in these types of studies requires a solid knowledge of the fossil plants in question, and caution must be taken when using isolated organs to infer times of origin/divergence of clades (Crane et al. 2004; Magallón 2004). In a similar way, phylogenetic studies of conifers that include fossil representatives require solid evidence of these taxa based on whole plant reconstructions. The use of fragmentary conifer organs such as isolated lateral branches or only cones tends to bias interpretations of taxonomic affinities (Rothwell and Mapes 2001; Rothwell et al. 2005; chapters 2-5 in this dissertation), probably giving false phylogenetic signals when compared to other conifers that are known as complete plants.

Fossil plants are essential for inferring phylogenetic relationships among plant groups and should not be relegated to serving only as proxies for the calibration of evolutionary rates for extant taxa. Most recent phylogenetic analyses fail to include fossil taxa that may represent stem or crown taxa. Fossil stem and crown taxa may play an important role in resolving deep nodes in conifer phylogeny and the lack of them in current phylogenetic inferences only adds confusion to the known discordant topologies of seed plants, arising from different gene sequences, codon positions, sequence alignments, etc. (i.e., Shindo et al. 1999; Winter et al. 1999; Bowe et al. 2000; Chaw et al. 2000; Magallón and Sanderson 2002; Burleigh and Mathews 2004).

Traditionally, conifers have been defined by the following diagnostic characters: simple leaves on vegetative branches, endarch pycnoxylic wood with circular bordered pits, simple pollen cones, and compound ovulate cones (Pilger 1926; Chamberlain 1935; Gifford and Foster 1987; Taylor and Taylor 1993; Stewart and Rothwell 1993). However, this circumscription fails to provide synapomorphies for both extant and extinct conifers. If our analysis is correct and all these primitive conifers are monophyletic, this would indicate that the current definition of conifers should be expanded to include characters present in primitive conifers, e.g., compound pollen cones, adaxial pollen sacs, monosaccate and monolete prepollen, compound ovulate zones, and sporophylls with erect or inverted ovules.

Our present knowledge of the most primitive conifers has improved greatly, but we still lack of synapomorphies that unite both extant and extinct conifers. A similar challenge highlighted by this study will likely occur in younger sediments (Mesozoic and Cenozoic), where conifers appear more diverse than in the Paleozoic. Additionally, more studies on the anatomy and development of living conifers will be needed to understand the different groups. Once we obtain these characters, familial circumscriptions can be modified, and clear diagnostic characters can be defined at the family level for fossil conifers. Such conifer species will be more useful in assessing phylogenetic relationships between fossil and living conifers, and in understanding their role in seed plant phylogeny.

Tables

Table 6-1. Taxonomic concepts of primitive conifers used in the phylogenetic analysis.

Taxa	Authority	Age/Region
[1]*Callistophyton poroxyloides*	Delevoryas and Morgan	Late Pennsylvanian/Euramerica
[2]*Cordaixylon dumusum*	Rothwell & Warner	Late Pennsylvanian/Euramerica
[3]*Mesoxylon priapii*	Trivett & Rothwell	Late Pennsylvanian/Euramerica
[4]*Barthelia furcata*	Rothwell & Mapes	Late Pennsylvanian/Euramerica
[5]*Emporia cryptica*	Hernandez-Castillo, Stockey, Rothwell & Mapes	Late Pennsylvanian/Euramerica
[6]*Emporia lockardii*	(Mapes & Rothwell) Hernandez-Castillo, Stockey, Rothwell & Mapes	Late Pennsylvanian/Euramerica
[7]*Emporia royalii*	Hernandez-Castillo, Stockey, Rothwell & Mapes	Late Pennsylvanian/Euramerica
[8]*Hanskerpia hamiltonensis*	Rothwell, Mapes & Hernandez-Castillo	Late Pennsylvanian/Euramerica
[9]Vojnovskya plant	Rothwell, Mapes & Mapes	Late Pennsylvanian to Early Permian/Euramerica
[10]*Ernestiodendron filiciforme*	(Florin) Florin	Early Permian/Euramerica
[11]*Otovicia hypnoides*	(Florin) Kerp, Swinkels, & Verweer	Early Permian/Euramerica
[12]*Utrechtia floriniformis*	(Mapes & Rothwell) Rothwell & Mapes	Early Permian/Euramerica
[13]*Thucydia mahoningensis*	Hernandez-Castillo, Rothwell & Mapes	Early Permian/Euramerica
[14]*Dicranophyllum hallei*	Remy & Remy	Early Permian/Euramerica
[15]*Concholepis harrisii*	Meyen	Early to middle Permian/Angara
[16]*Kungarodendron sharovii*	Meyen	Early to middle Permian/Angara
[17]*Timanostrobus muravievii*	Meyen	Early to middle Permian/Angara
[18]*Ferugliocladus patagonicus*	(Feruglio) Archangelsky & Cuneo	Mid-Permian/Gondwana
[19]*Genoites patagonica*	Feruglio	Mid-Permian/Gondwana
[20]*Dolomitia cittertiae*	Clement-Westerhof	Late Permian/Euramerica
[21]*Majonica alpina*	Clement-Westerhof	Late Permian/Euramerica
[22]*Ortiseia leonardii*	Florin	Late Permian/Euramerica
[23]*Voltzia hexagona*	(Bischoff) Geinitz	Late Permian/Euramerica
[24]*Aethophyllum stipulare*	Brongniart	Middle Triassic/Euramerica

1. Rothwell (1975, 1980, 1981). 2. Rothwell and Warner (1984) and Rothwell (1993). 3. Trivett and Rothwell (1985). 4. Rothwell and Mapes (2001). 5. Hernandez-Castillo,

Stockey, Rothwell and Mapes (2005). 6. Mapes and Rothwell (1991, 2003) and Hernandez-Castillo, Stockey, Rothwell and Mapes (2005). 7. Hernandez-Castillo, Stockey, Rothwell and Mapes (2005). 8. Rothwell, Mapes and Hernandez-Castillo (2005). 9. *Vojnovskya* Neuberg (1955), *Vojnovskya* plant sensu Rothwell, Mapes, and Mapes (1996). 10. Florin (1938-45), concept of this species is based primarily on Florin, with the exception of scoring the ovules as inverted sensu Clement-Westerhof (1984). 11. Kerp et al. (1990) but we have scored pollen sac position as unknown and reexamination is needed. 12. Mapes and Rothwell (1991) and Rothwell and Mapes (2003). 13. Hernandez-Castillo, Rothwell, and Mapes (2001). 14. Barthel (1977), sensu Rothwell and Mapes (2001). 15-17. Meyen (1997). 18. Archangelsky and Cuneo (1987). 19. Cuneo (1985). 20-21. Clement-Westerhof (1987). 22. Florin (1964) sensu Clement-Westerhof (1984). 23. Schweitzer (1996). 24. Grauvogel-Stamm (1978).

Table 6-2. Current classifications of the most ancient conifers.

Mapes and Rothwell		Clement-Westerhof, Visscher and Kerp	
Family	**Genera**	**Family**	**Genera**
Utrechtiaceae	*Utrechtia* Mapes and Rothwell *Ortiseia* Florin *Moyliostrobus* Miller and Brown *Ernestiodendron* Florin *Otovicia* Kerp et al.	Walchiaceae	*Walchia* Sternberg *Ortiseia* Florin *Moyliostrobus* Miller and Brown *Ernestiodendron* Florin *Otovicia* Kerp et al. *Walchiostrobus* Florin *Culmitzchia* Ullrich
Emporiaceae	*Emporia* Mapes and Rothwell *Hanskerpia* Rothwell et al.		
Ullmaniaceae	*Ullmania* Goeppert	Ullmaniaceae	*Ullmania* Goeppert
Thucydiaceae	*Thucydia* Hernandez-Castillo et al.		
Majonicaceae	*Majonica* Clement-Westerhof *Dolomitia* Clement-Westerhof	Majonicaceae	*Majonica* Clement-Westerhof *Dolomitia* Clement-Westerhof *Pseudovoltzia* Florin
Voltziaceae	*Voltzia* Brongniart		
Angaran conifers	*Concholepis* Meyen *Kungarodendron* Meyen *Timanostrobus* Meyen		
Ferugliocladaceae	*Ferugliocladus* Archangelsky and Cuneo *Genoites* Cuneo		
Morphotaxa	*Walchia* Sternberg *Culmitzchia* Ullrich *Walchiostrobus* Florin *Gomphostrobus* Marion *Lecrosia* Florin *Feysia* Broutin and Kerp *Cassinisia* Kerp et al.	Morphotaxa	*Walchianthus* Florin *Thuringiostrobus* Kerp and Clement-Westerhof *Hermitia* Broutin and Kerp emend. *Feysia* Broutin and Kerp *Cassinisia* Kerp et al.

Table modified from Mapes and Rothwell 1991.

Appendices

Appendix 6-1. Characters and character states of primitive conifers and coniferophytes used in the analysis.

# Characters and character states

1. Orthotrophic branching of stem (0) absent, (1) present.
2. Ultimate branch arrangement (0) irregular/three dimensional, (1) plagiotrophic (pinnate).
3. Leaf dimorphism on the same branches (0) present, (1) absent.
4. Leaves on penultimate branches different from leaves on ultimate branches (0) absent, (1) present. See Meyen, 1997, p. 428 - i.e., forked leaves on penultimate shoots.
5. Bud scales (0) absent, (1) present.
6. Heteroblasty (0) absent or slight, (1) prominent. See Meyen, 1997, p. 429.
7. Vegetative leaf (0) relatively narrow with one or two veins, (1) strap-shaped with more than two veins, (2) pinnate with dichotomous venation.
8. Vegetative leaf form (0) straight or flexuous, (1) slightly concave, (2) S-shaped bending toward stem, (3) spreading, (4) falcate, (5) linear, (6) slightly lanceolate. After Hernandez-Castillo et al., 2001a.
9. Leaves narrowing toward base (0) absent, (1) present. See Meyen, 1997, p. 429.
10. Leaf in cross-section (0) rhomboid and transversely elongated, (1) ellipsoidal with larger, convex adaxial face, (2) thin and flattened, (3) vertically elongated, diamond-shaped. See Meyen, 1997 p. 429.
11. Leaf (or leaf segment) apex (0) pointed, (1) rounded, (2) mucronate. See Meyen, 1997, in part.
12. Leaf cushions or consistently shaped leaf scars (0) absent, (1) present.
13. Margin of leaves on ultimate branches (0) more or less entire, (1) dissected less than 1/3 distance from base to apex, (2) dissected more than ½ distance to apex.
14. Margin of leaves on ultimate branches (0) more or less entire, (1) dissected less than 1/3 distance from base to apex, (2) dissected more than ½ distance to apex.
15. Leaf margin (0) smooth, (1) with uniseriate trichomes, (2) toothed (at least biseriate immediately distal to base).
16. Adaxial stomata (0) absent, (1) two bands, (2) multiple bands, (3) uniseriate rows, (4) scattered.
17. Abaxial stomata (0) absent, (1) two bands, (2) multiple bands, (3) uniseriate rows, (4) scattered.
18. Subsidiary cell positions (0) surrounding guard cells, (1) lateral and often polar to guard cells.

19. Dicyclic stomata (0) absent, (1) present (at least in part).

20. Subsidiary cells with prominent papilla overarching guard cells (0) present, (1) absent.

21. Surficial trichomes (0) present, (1) absent.

22. Pollen cone position (0) terminating leafy branch, (1) lateral in axil of leaf. Following positions of ovulate structures. 23. Pollen cones (0) simple shoots, (1) compound shoots.

24. Microsporophyll with shank and distal lamina (0) present, (1) absent.

25. Microsporophyll morphology (0) linear, (1) with bilateral distal lamina, (2) with radial distal lamina (peltate), (3) with entire sporophyll laminar.

26. Microsporophyll distal lamina with basal keel (0) absent, (1) present. See Meyen, 1997, p. 425.

27. Microsporophyll apex (0) single, (1) forked.

28. Pollen sac attached to (0) tip of sporophyll, (1) sporophyll stalk, (2) distal lamina of sporophyll, (3) adaxial surface of lamina. See Meyen, 1997, p. 425. Character state (3) refers to the surface of sporophylls that are not differentiated into a narrow stalk and distal lamina (see Character 25).

29. Adaxial pollen sac attachment (0) absent, (1) present.

30. Microgametophytes with proximal suture (0) present, (1) absent.

31. Microgametophytes with distal aperture (0) absent, (1) present.

32. Protosacci of pollen (0) absent, (1) present.

33. Eusacci of pollen (0) absent, (1) present.

34. Ultimate ovule bearing unit (0) leaf, (1) stem.

35. Ovule or ovulate fructification (ultimate ovule bearing unit = UOU) produced at apex of vegetative branch (0) absent, (1) present. This is opposed to being lateral or axillary, and is scored as present even if the apex grows through to be vegetative later.

36. Number of ovules per UOU (ultimate ovule bearing unit) (0) >1, (1) 1.

37. Fertile aggregations determinant (0) absent, (1) present. (i.e., forming a cone in which the apical meristem is used up).

38. Bract (= leaf) subtending ovule or ovulate cone (0) similar to vegetative leaf, (1) modified as compared to vegetative leaf.

39. Bract/ovuliferous structure (0) free, (1) fused at base only, (2) fused for >2/3.

40. Forked bract (0) present, (1) absent. See Meyen, 1997.

41. Bract with marginal trichomes (0) absent, (1) present.

42. Marginally dentate bract (0) absent, (1) present.

43. Axillary shoot/ovuliferous scale (0) radial, (1) flattened. See Meyen, 1997.

44. Ovules produced (0) from all sides of shoot, (1) adaxially (i.e., facing apex of stem upon which axillary shoot is borne) and laterally, (2) from lateral sides of shoot only, (3) from adaxial side of shoot only. See Clement-Westerhof, 1987 and Meyen, 1997, p. 415.

45. Ovules (0) erect, (1) inverted.

46. Ovules borne on visible sporophylls (0) present, (1) absent.

47. Ovules borne on more-or-less fused structure that may represent a single sporophyll or several sporophylls and vegetative scales (i.e., "fertile scales" of some authors; Mapes & Rothwell, 1991) or on an ovuliferous scale (0) absent, (1) present.

48. Ovules borne on sporophyll/fertile scale/ovuliferous scale (0) apically/marginally, (1) surfically, near tip, (2) surficially, midrigion, (3) surficially, near base.

49. Number of potentially fertile ovules per ovuliferous shoot/ovuliferous scale usually (1) numerous, (1) variable <eight, (2) three, (3) two, (4) one.

50. Vegetative scales on ovuliferous shoot (0) numerous, >20, (1) several, 6-20, (2) few, 1-5, (3) absent.

51. Intergrading vegetative and fertile scales (0) absent, (1) present

52. Vegetative scales on adaxial surface of ovuliferous shoot (0) present, (1) absent.

53. Vegetative scales on abaxial surface of ovuliferous shoot (0) present, (1) absent.

54. Sporophylls aggregated at apex of shoot (0) present, (1) absent. See Meyen, 1997.

55. Ovules with two apical lobes or projections (0) absent, (1) present.

56. Ovules with chalazal extensions (horns, lobes, etc.) (0) absent, (1) two extensions, (2) three extensions, (3) one, wing-like extension.

57. Ovules with coarse exterior trichomes (0) absent, (1) present.

Appendix 6-2. Character matrix used in phylogenetic analysis of walchian conifers.

Taxa/Characters	10	20	30	40	50	57
Callistophyton poroxyloides	1020101011	10110?????	000010?201	1010000000	0000000003	102010
Cordaixylon dumusum	111010	1100020100	012000?001	10001100	0 00000010	111010
Mesoxylon priapii	101010	1100020100	012000?000	10011100	0000000000	101010
Barthelia furcata	?01(0,1)000100	001(0,1)110001	1211111110	10010001	100??00040	?01(0,1)000100
Emporia cryptica	1111000(0,5)00	10213021	1200110110	10011110	101(1,3)100(0,1)10	1111000(0,5)00
Emporia lockardii	1101000(1,2)00	001021(3,4)001	1211110110	10011101	1013100010	1101000(1,2)00
Emporia royalii	1111000(0,2)00	10213001	1211110110	10011111	1013100(0,1)10	1111000(0,2)00
Hanskerpia hamiltonensis	?101000100	10033001	1????????0	10011011	1113100030	?101000100
Vojnovskyean plant	?000??1012	1100?02???	??????????	???0111?0?	?000000000	?000??1012
Ernestiodendron filiciforme	110000030?	133011	?21?110??0	10101000	??13100011	110000030?
Otovicia hypnoides	?1(0,1)(0,1)000400	114011	12111101?0	100011101	1013100131	?1(0,1)(0,1)000400
Utrechtia floriniformis	1101000(1,2)0?	00(0,1)0111001	1?????????	???0111101	13100140	1101000(1,2)0?
Thucydia mahoningensis	1100000(1,2)01	210001	122000?000	10110000	113100011	1100000(1,2)01
Dicranophyllum hallei	0000000 0030	122201100	0?????????	???0?10000	000??00?10	?10?00????
Concholepis harrisii	?000000(2,4)02	01001?????	??????????	???0???000	??13???000	?000000(2,4)02
Kungurodendron sharovii	?100000(1,5)00	10001	1?1?100??0	010011?000	??13100000	100????
Timanostrobus muravievii	?000000102	144000	0?1??????0	01001?1000	??00000000	?000 0001?0?
Feruglioclodus spp.	100	44000	0210110011?	?011111000	0004010 043	1100
Genoites patagonica	?010010103	01110?????	??????????	???1111001	4010043	111000
Dolomitia cittertiae	??1??00?0?	1000134001	??????????	???01?1100	??11111(2,3)21	??1??00?0?
Majonica alpina	??10?0061?	1000033001	0?1?11???0	10111110	111111331	??10?0061?
Ortiseia spp.	?100000100	(0,1)000033011	1?1?11???0	10111000	13111240	?100000100
Voltzia hexagona	?001000103	01000?????	??11110???	???0110100	13111220	?001000103
Aethophyllum stipulare	11002	10000?????	211110111	1010111110	?013111213	110000

Data modified from Rothwell et al. (2005).

Figure Legends

Fig. 1. Strict consensus of two most parsimonious trees of 185 steps. Values above branches are bootstrap values, below are jacknife values, and to right of branches are decay values. Note major clades including Cordaitalean clade, conifer clade and voltzialean conifer clades (Angaran, Gondwanan, Voltzian and Lebachioid).

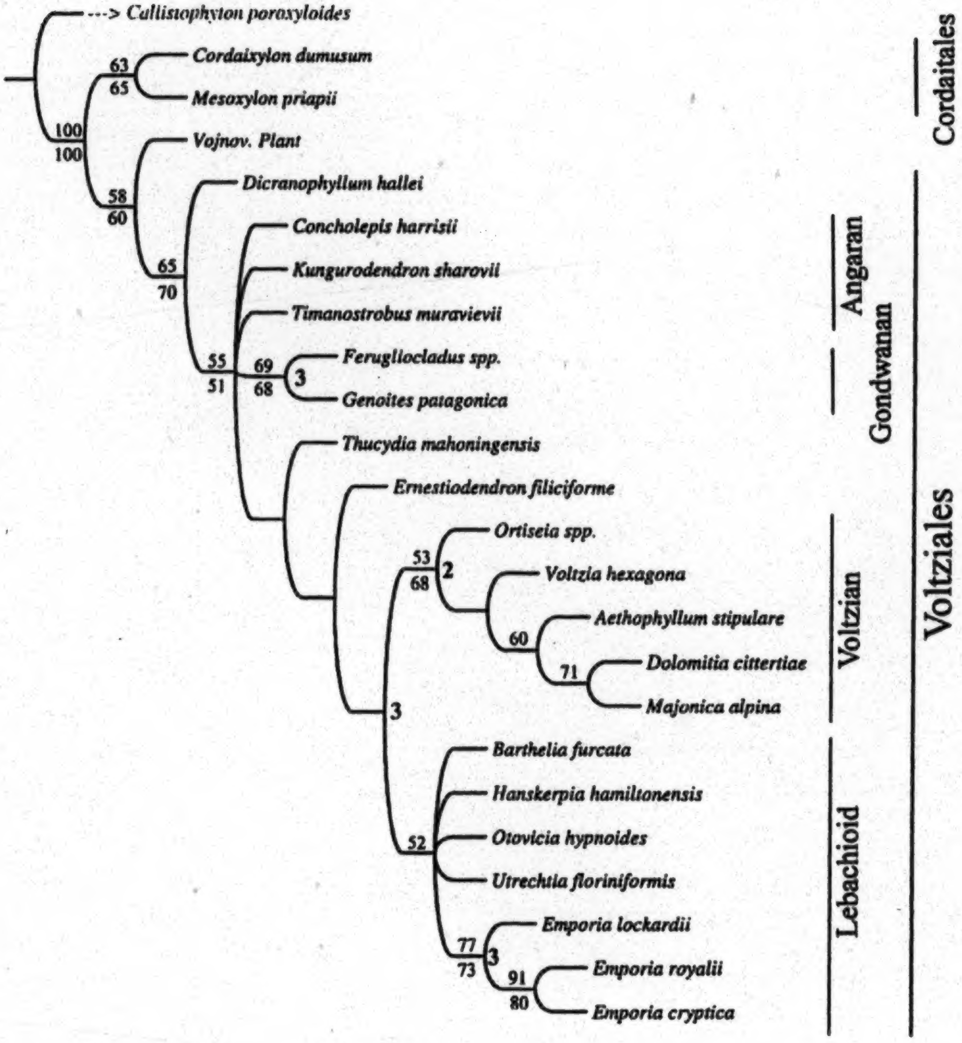

---> Callistophyton poroxyloides
Cordaixylon dumusum
Mesoxylon priapii
Vojnov. Plant
Dicranophyllum hallei
Concholepis harrisii
Kungurodendron sharovii
Timanostrobus muravievii
Ferugliocladus spp.
Genoites patagonica
Thucydia mahoningensis
Ernestiodendron filiciforme
Ortiseia spp.
Voltzia hexagona
Aethophyllum stipulare
Dolomitia cittertiae
Majonica alpina
Barthelia furcata
Hanskerpia hamiltonensis
Otovicia hypnoides
Utrechtia floriniformis
Emporia lockardii
Emporia royalii
Emporia cryptica
63
65
100
100
58
60
65
70
55
51
69
68
3
53
68
2
60
71
3
52
77
73
3
91
80
Cordaitales
Angaran
Gondwanan
Voltzian
Lebachioid
Voltziales

Fig. 2. Strict consensus of two most parsimonious trees of 185 steps showing characters (values above branches) and character states (below branches) for all nodes.

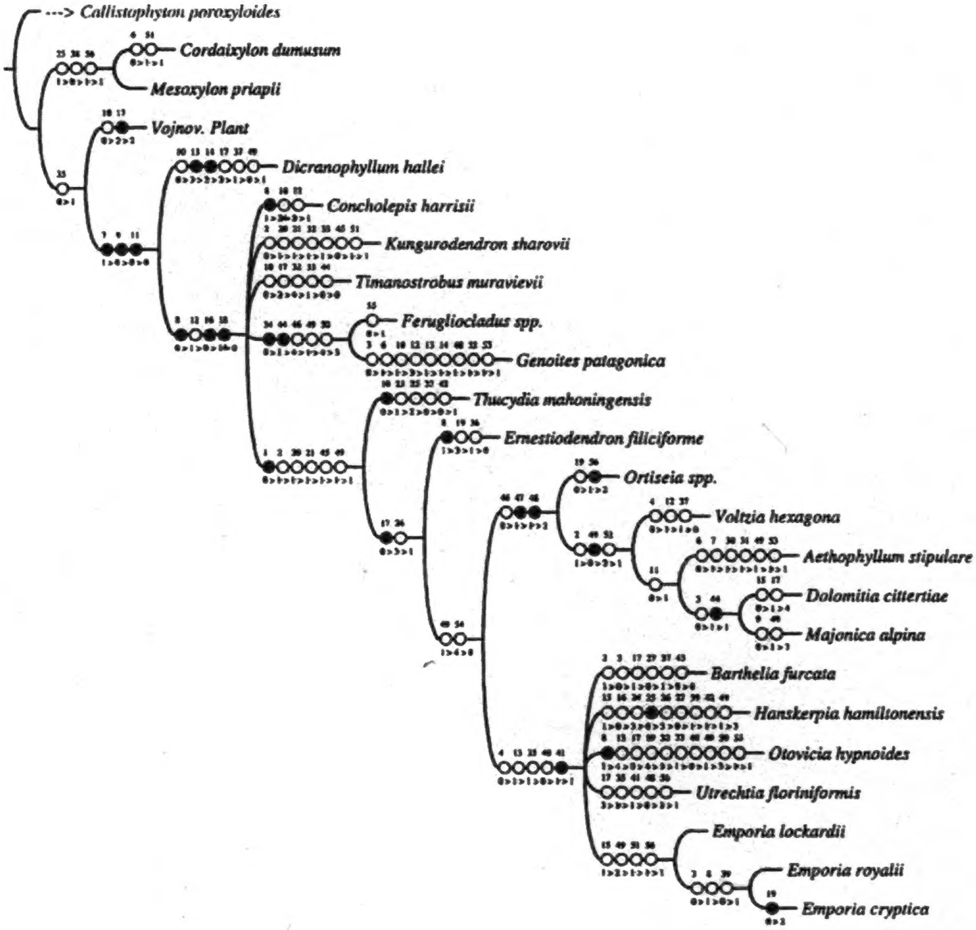
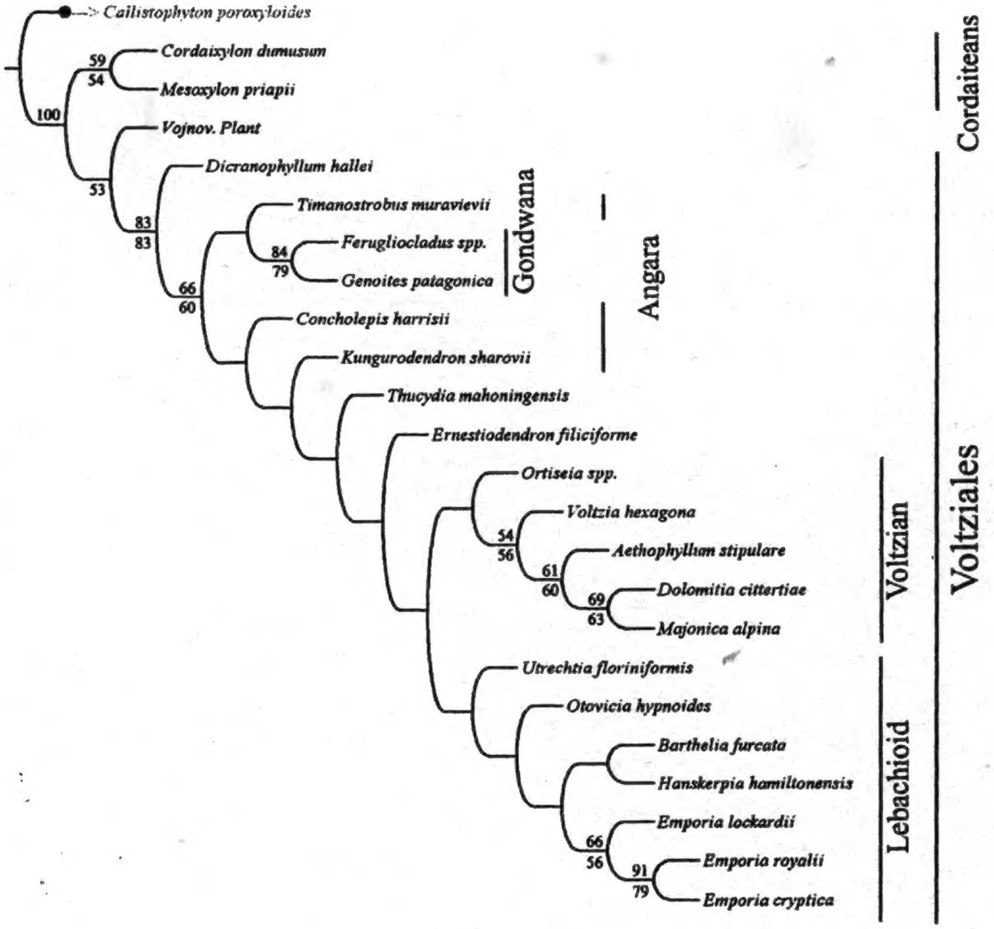

---> Callistophyton poroxyloides
Cordaixylon dumusum
Mesoxylon priapii
Vojnov. Plant
Dicranophyllum hallei
Concholepis harrisii
Kungurodendron sharovii
Timanostrobus muravievii
Ferugliocladus spp.
Genoites patagonica
Thucydia mahoningensis
Ernestiodendron filiciforme
Ortiseia spp.
Voltzia hexagona
Aethophyllum stipulare
Dolomitia cittertiae
Majonica alpina
Barthelia furcata
Hanskerpia hamiltonensis
Otovicia hypnoides
Utrechtia floriniformis
Emporia lockardii
Emporia royalii
Emporia cryptica

Fig. 3. Most parsimonious tree of 141 steps showing all nodes resolved after removal of nine characters (6, 10, 12 , 15, 16, 32, 33, 52, and 53). Note Gondwanan Voltziales clade and *Timanostrobus muravievii* form clade sister to all other Voltziales and Lebachioid clade that is fully resolved. Number values above branches are bootstrap values, below branches are jacknife values, and to right of branches are decay values.


Callistophyton poroxyloides
Cordaixylon dumusum
Mesoxylon priapii
Vojnov. Plant
Dicranophyllum hallei
Timanostrobus muravievii
Ferugliocladus spp.
Genoites patagonica
Concholepis harrisii
Kungurodendron sharovii
Thucydia mahoningensis
Ernestiodendron filiciforme
Ortiseia spp.
Voltzia hexagona
Aethophyllum stipulare
Dolomitia cittertiae
Majonica alpina
Utrechtia floriniformis
Otovicia hypnoides
Barthelia furcata
Hanskerpia hamiltonensis
Emporia lockardii
Emporia royalii
Emporia cryptica
59
54
100
53
83
83
66
60
84
79
54
56
61
60
69
63
66
56
91
79
Gondwana
Angara
Voltzian
Lebachioid
Cordaiteans
Voltziales

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CHAPTER 7

Conclusions

Introduction

The content of this dissertation attempt to tackle a problem that has been at the forefront of conifer systematics since the time of Florin (1927, 1938-45, 1950, 1951). Although, Florin made a monumental contribution by synthesizing the current knowledge of ancient conifers, more recent advances have rejected several of his assumptions (Schweitzer 1963; Cuneo 1985; Archangelsky and Cuneo 1987; Clement-Westerhof 1984; Mapes and Rothwell 1984, 1991, 1998, 2003; Kerp et al. 1990; Meyen 1997; Rothwell and Mapes 2001; Hernandez-Castillo et al. 2001a, 2001b). Results of this dissertation further refine our interpretations of Paleozoic conifers. Chapter two of this dissertation offers a new methodology to account for ranges of variation within species of fossil conifers using mutivariate analyses. This methodology provides a framework to understand growth architecture of fossil conifers and is calibrated using a comparison to juvenile trees of extant *Araucaria heterophylla* (Salisb.) Franco.

Chapters three to five include whole plant reconstructions from the Upper Pennsylvanian of Kansas. Due to the large number of fossil specimens and the great variability observed, the family Emporiaceae, the genus *Emporia,* and *Emporia lockardii* were emended in the process of describing two new species. Using individual organ comparisons, the Hamilton Quarry specimens overlap considerably. However, organs can be correlated by means of organic connection and morphological, cuticular and anatomical characters. These correlations result in clear sets of diagnostic characters that can be used to typify whole plant species.

Caution must be taken when analyzing isolated pollen cones. Microsporophylls in these new species overlap in size and shape depending on the developmental stage of the cone. Several cones are needed to differentiate mature microsporophylls, and these can then be used to distinguish different species by their cones. Similarly, prepollen grains in the three *Emporia* species show a large diversity in size and shape that is comparable to that found by Bharadwaj (1964). Prepollen of referable to several species has been found in one cone. An in depth analysis of the prepollen grains from *Emporia* pollen cones in needed.

The *Emporia* species described here provide the earliest evidence of age-dependent heterophylly in ancient conifers and support previous ideas on the reproductive biology of Paleozoic conifers (Mapes and Rothwell 1984). All three species of Emporiaceae are now known as whole plants.

The Emporiaceae is one of the two families where all cuticles of leaves and leaf-like structures have been fully analyzed. Cuticular features of these species show that all leaves in a single plant have a basic stomatal structure, distribution, number of stomata per band, and number of subsidiary cells per stomata, but this basic pattern varies among the different organs of the plant (Table 1, chapters 3-5). This confirms that cuticles from isolated and/or fragmentary branches, where no organic connections and/or small number of specimens are known, are not useful to accurately identify walchian conifers.

Chapter six builds on previous reconstructions and presents a phylogenetic analysis on the relationships of the most primitive conifers. This analysis suggests a single clade that includes all of the most ancient conifers and places them as sister to the Late Carboniferous Cordaitales and a transitional conifer-like *Vojnovskya* plant. The base of the Voltziales clade is characterized by a polytomy that includes Angaran, Gondwanan conifers, and *Thucydia*, and *Ernestiodendron* at the base of a paraphyletic assemblage of

Euramerican conifers.

Conclusions by chapter

Chapter 2

A new approach based on multivariate analysis was tested with *Thucydia mahoningensis*, the first species of primitive conifers where morphological ranges of variation were recorded. Cluster (CA) and principal component analyses (PCA) were used and two basic types of lateral branches distinguished. These branches are either small with a deltoid shape or large with an ovoid shape, and are similar to lateral branches of juvenile individuals of *Araucaria heterophylla*. Application of this multivariate approach provides a new method for identifying diagnostic characters of primitive conifers. *Thucydia mahoningensis* produced an orthotropic monopodial stem with regular tiers of vegetative plagiotropic branches that bear well-developed ultimate shoots (Hernandez-Castillo et al. 2003). Trees with a monopodial stem and series of regular plagiotropic branches conform to Massart's model of tree architecture (Hallé and Oldeman 1970; Hallé et al. 1978; Veillon 1978). These include both *T. mahoningensis* and *A. heterophylla* (Hernandez-Castillo et al. 2003). Therefore, a detailed analysis of the ranges of variation of *A. heterophylla* produce a tree architecture and growth model that can be used to correlate and compare primitive conifer remains.

Individual analyses using *A. heterophylla* suggest that juvenile trees have at least seven different types of lateral branches that can be differentiated by the length of penultimate shoot (LPS), thickness of leaves at proximal region of the ultimate shoot (TBU), angles of divergence at the proximal and distal regions of the ultimate shoot (A1A, A2A, A1B, A2B), and the number of ultimate shoots (NUS). These lateral branches can be differentiated using branch size, shape, and position. Multivariate analyses of fossil taxa indicates that *Lebachia piniformis* specimens from Germany can be accurately differentiated from *Thucydia*, *Ernestiodendron*, and *L. piniformis* specimens from France. Species differentiation is based on the same set of characters found in previous analyses using only *A. heterophylla*. Clearly it is possible to differentiate *Araucaria*, *Thucydia*, *Ernestiodendron*, and lebachioid species from France by using multivariate analyses. While discrete clusters of fossil species are present, individual specimens do not cluster in a manner equivalent to that found in *Araucaria*, where size, shape and position governs the orders of branching. The species with the greatest number and variety of lateral branches (*Thucydia*) is clearly the most delimited of the fossils in the analysis, suggesting a similar growth architecture to that of living araucarians (Hernandez-Castillo et al. 2003). This pioneering multivariate analysis involved more characters (14) and species (25) than any previous study (Bertholon 1996). My study shows conclusively that multivariate analysis of this kind can aid in differentiating species of fossil conifers but is limited by preservation and the number of specimens available. Caution should be taken when reconstructing fossil conifers and if these kinds of analyses are used, they should be combined with reliable organ correlations.

Chapter 3

Emporia lockardii has lateral plagiotropic branches with simple and forked leaves, simple pollen cones, and compound ovulate cones. Stems have an endarch eustele with dense wood surrounding a septate pith. Leaves display age-dependent heterophylly, and are amphistomatic with two adaxial stomatal bands, papillate epidermal cells, and two longitudinal, short, basal, narrow, abaxial bands, or individual rows of stomata with numerous trichome bases. Pollen cones have helically arranged peltate microsporophylls and adaxial pollen sacs. Prepollen is monolete, monosaccate (*Potonieisporites* Bharadwaj). Ovulate cones are compound with helically arranged, forked bracts that bear bilaterally symmetrical axillary dwarf shoots with numerous sterile scales and one to three narrow megasporophylls. Ovules are terminal, inverted, and bilateral. These characters lead to a reevaluation of the family and a subsequent emendment of its diagnosis.

Chapter 4

Emporia cryptica extends our knowledge of the ranges of variation within a single walchian conifer. This conifer has lateral plagiotropic branches with simple leaves, simple pollen cones, and compound ovulate cones. Stems have an endarch eustele with dense wood surrounding a septate pith, and secondary tracheids with multiseriate hexagonal bordered pits. Leaves are amphistomatic with two adaxial stomatal bands of monocyclic stomata, scattered dicyclic stomata, and papillate epidermal cells, and two, narrow, abaxial rows of stomata with numerous trichome bases. Pollen cones are simple and have helically arranged microsporophylls and adaxial pollen sacs. Prepollen is monolete, monosaccate (*Potonieisporites* Bharadwaj). Ovulate cones are compound with bilaterally symmetrical axillary dwarf shoots that have numerous sterile scales (up to 25), two megasporophylls, and occur in the axils of helically arranged, forked bracts. Each megasporophyll bears a single inverted ovule. *Emporia cryptica* is the only walchian conifer where immature and mature embryos have been found, demonstrating that the most ancient conifers already possessed seed dormancy.

Chapter 5

Emporia royalii has lateral plagiotropic branches with simple and forked leaves, age-dependent heterophylly, simple pollen cones, and compound ovulate cones. Stems have an endarch eustele, dense wood and sclerotic nests in the pith. Leaves are amphistomatic with two adaxial stomatal bands, and two longitudinal abaxial rows of stomata with numerous trichome bases. Pollen cones are simple and have helically arranged microsporophylls and adaxial pollen sacs. Prepollen is monolete and monosaccate (*Potonieisporites* Bharadwaj). Ovulate cones are compound with bilaterally symmetrical axillary dwarf shoots that bear up 40 sterile scales and 1-2 sporophylls, and occur in the axils of helically arranged bracts with forked tips. Ovules are inverted, winged, and resemble those of *E. lockardii* and *E. cryptica*. This is the last conifer reconstruction at the Hamilton Quarry making it the only locality in the world where all conifers have been described as complete plants.

Chapter 6

Support for the trees in the phylogenetic analysis is extremely low with the exception of the Gondwanan, Voltzian and Emporiaceae clades. The Emporiaceae clade exemplifies the importance of whole plant reconstructions to the resolution of long-debated systematic problems. Morphotaxa do not reflect whole plants and, thus, are unreliable in the assessment of phylogeny. Characters supporting Voltziales are needle-like leaves and stomata with subsidiary cells encircling guard cells. The Gondwanan clade is supported by single terminal ovules borne on axillary dwarf shoots that lack distinct sporophylls and sterile scales. Voltzian conifers have ovules on visible sporophylls that are fused to other structures on the axillary dwarf shoot. The Emporiaceae shares dissimilar penultimate and ultimate shoots and forked bracts on ovulate cones.

Concluding remarks

Methodologies used so far to assess systematic relationships of ancient conifers are inadequate. Even though more than 70 species of walchian conifers have been described worldwide we only know a handful of these taxa as complete plants. More taxa need to be reconstructed to understand how these plants are related to other fossil and extant conifers. Knowledge of the morphological, cuticular, anatomical, growth architectural and reproductive characters of these plants will help to quantify variation and character recognition, and to allow for a more accurate coding in future phylogenetic analyses of fossil and extant conifers.

Traditionally, conifers have been defined by the following diagnostic characters: simple leaves on vegetative branches, endarch pycnoxylic wood with circular bordered pits, simple pollen cones, and compound ovulate cones (Pilger 1926; Chamberlain 1935; Gifford and Foster 1987; Taylor and Taylor 1993; Stewart and Rothwell 1993). This current definition of conifers should be expanded to include characters present in primitive conifers, such as compound pollen cones, adaxial pollen sacs, monosaccate and monolete prepollen, compound ovulate zones, and sporophylls with erect or inverted ovules.

Our present knowledge of the most primitive conifers has improved greatly, but we still lack synapomorphies that unite both extinct and extant conifers. There is a large number of yet undescribed species and disorganized morphotaxa in younger sediments that are in need of whole plant reconstructions to reveal characters that are otherwise cryptic, as in Paleozoic conifers. An appreciation for these characters would greatly enhance the knowledge of not only fossil conifers, but will also illuminate the significance of features in living conifers that have been previously overlooked. Current familial circumscriptions need to be modified so that clear diagnostic characters can be defined at the family level among fossil conifers.

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APPENDICES

Appendix 1. Important European collections with walchian conifers and most common species per collection. Forty-five of them were used in preliminary multivariate analyses.

Species	**Authority**	**Stock**	**Montp**	**Schleus**	**Berlin**	**Paris**	**Prague**	**Fran**	**Dresden**	**Gotha**
Lebachia piniformis	Florin	23	30	68	33		2	4		7
Walchia filiciformis	Sternberg	2				8		3	8	
Lebachia frondosa	(Renault) Florin	2	9						4	
Lebachia geoppertiana	Florin	2	1							
Walchia (Ernestodendron) arnhadtii	Florin	2			1					
Lebachia laxifolia	Florin	10	4	14						
Walchia arnhadtii	Florin									
Lebachia speciosa	Florin				3		1			
Lebachia hypnoides	(Brongniart) Florin	5	25	10	7	7		1		
Walchia germanica	Florin	3						2		
Lebachia parvifolia	Florin	5		17	10		2			
Ernestiodendron filiciforme	(Sternberg) Florin	6			8					
Walchia (Ernestodendron) germanica	Florin	2								
Lebachia goeppertiana	Florin	2								
Walchia schlotheimii	(Brongniart) Florin	1	3			3				
Walchia (Lebachia?) bertrandii	Florin		2							

A complete list of museums can be found in chapter two. Stock = Stockholm. Montp = Montpellier. Schleus = Schleusingen. Fran = Frankfurt.

Appendix 2. Walchian conifer specimens observed and photographed.

Species	Authority	Museum
Ernestiodendron		Staatl Museum Min. Geol.
Ernestiodendron		Staatl Museum Min. Geol.
Ernestiodendron		Staatl Museum Min. Geol.
Ernestiodendron (cf Ernestiodendron)		Staatl Museum Min. Geol.
Ernestiodendron, Dicranophyllum and W. piniformis		Staatl Museum Min. Geol.
Ernestiodendron filiciforme	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Ernestiodendron filiciforme	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Ernestiodendron filiciforme		Czech Geological Survey
Ernestiodendron filiciforme		Czech Geological Survey
Ernestiodendron filiciforme		Czech Geological Survey
Ernestiodendron filiciforme		Czech Geological Survey
Ernestiodendron filiciforme	(Sternberg) Florin	Narodni Museum
Ernestiodendron filiciforme	(Sternberg) Florin	Narodni Museum
Ernestiodendron filiciforme	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Ernestiodendron filiciforme	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Ernestiodendron filiciforme	(Schlotheim) Florin	Staatl Museum Min. Geol.
Ernestiodendron filiciformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Ernestiodendron filiciformis	(Schlotheim) Florin	Naturhistorisches Museum Schloss Bartholdsburg
Ernestiodendron filiciformis var gracilis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Ernestiodendron piniformis		Czech Geological Survey
Lebachia		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia ?		Staatl Museum Min. Geol.
Lebachia frondosa	(Renault) Florin	Staatl Museum Min. Geol.
Lebachia frondosa	(Renault) Florin	Staatl Museum Min. Geol.
Lebachia frondosa	(Renault) Florin	Staatl Museum Min. Geol.
Lebachia frondosa	(Renault) Florin	Staatl Museum Min. Geol.
Lebachia frondosa	Weissig	Staatl Museum Min. Geol.
Lebachia frondosa	Weissig	Staatl Museum Min. Geol.
Lebachia frondosa	Weissig	Staatl Museum Min. Geol.
Lebachia geoppertiana	Florin	Staatl Museum Min. Geol.
Lebachia geoppertiana	Florin	Narodni Museum
Lebachia goeppertiana	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia goeppertiana	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia goeppertiana	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia hynoides	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia hynoides ?	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia hynoides and L. piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia hypnoides	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia hypnoides		Museum der Natur Gotha
Lebachia hypnoides	Brongniart	Narodni Museum
Lebachia hypnoides	(Brongniart) Florin	Narodni Museum
Lebachia hypnoides	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia hypnoides	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia hypnoides (W piniformis)	Broumova id	Narodni Museum
Lebachia laxifolia	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia laxifolia	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia laxifolia	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia laxifolia	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia laxifolia	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia laxifolia	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia laxifolia	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia laxifolia	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia laxifolia	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia laxifolia	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia laxifolia	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia mitis	Florin	Narodni Museum
Lebachia parvifolia		Museum der Natur Gotha
Lebachia parvifolia	Florin	Narodni Museum
Lebachia parvifolia	Florin	Narodni Museum
Lebachia parvifolia	Florin	Narodni Museum
Lebachia parvifolia	Florin	Naturhistorisches Museum Schloss Bartholdsburg

Lebachia parvifolia		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia parvifolia	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia parvifolia	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia parvifolia before as piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Staatl Museum Min. Geol.
Lebachia piniformis	(Schloth.) Florin	Staatl Museum Min. Geol.
Lebachia piniformis		Staatl Museum Min. Geol.
Lebachia piniformis		Staatl Museum Min. Geol.
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Museum der Natur Gotha
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Naturhistoriska riksmuseet
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Montpellier II, Montpellier
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg

Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	(Sternberg) Florin	Narodni Museum
Lebachia piniformis	(Schlotheim) Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Lebachia piniformis		Staatl Museum Min. Geol.
Lebachia piniformis	(Schlotheim) Florin	Staatl Museum Min. Geol.
Lebachia piniformis (W piniformis Schlt)	(Sternberg) Florin	Narodni Museum
Lebachia piniformis, parvifolia,	Florin	Naturhistorisches Museum Schloss Bartholdsburg

germanica		
Lebachia sp.		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia sp.		Narodni Museum
Lebachia sp.	Weissig	Staatl Museum Min. Geol.
Lebachia sp. (Walchia)		Naturhistorisches Museum Schloss Bartholdsburg
Lebachia speciosa	Florin	Narodni Museum
Lebachia speciosa	Florin	Narodni Museum
Lebachia speciosa	Florin	Narodni Museum
Lebachia speciosa	Florin	Charles University, Katedra Paleontologie Prirodovedecke Fakalty U K
Lebachia speciosa	Bacov id	Charles University, Katedra Paleontologie Prirodovedecke Fakalty U K
Lebachia speciosa	Bacov id	Charles University, Katedra Paleontologie Prirodovedecke Fakalty U K
Licopodites bronni	Sternberg	Narodni Museum
Licopodites bronni	Sternberg	Narodni Museum
Pseudovoltzia liebeana	Geinitz	Staatl Museum Min. Geol.
Pseudovoltzia liebeana	(Geinitz) Florin	Staatl Museum Min. Geol.
Tylodendron sp.	Piplov? Id	Charles University, Katedra Paleontologie Prirodovedecke Fakalty U K
Ullmania bronii		Naturhistorisches Museum Schloss Bartholdsburg
Ullmania bronii		Museum fur Naturkunde
Ullmania bronni	Goeppert	Staatl Museum Min. Geol.
Ullmania bronni	Goeppert	Staatl Museum Min. Geol.
Ullmania frumentaria	Schlotheim	Staatl Museum Min. Geol.
Ullmania frumentaria	Geinitz	Staatl Museum Min. Geol.
Ullmania frumentaria	Schlotheim	Staatl Museum Min. Geol.
Ullmania frumentaria	Schlotheim	Staatl Museum Min. Geol.
Ullmania selaginoides	Geinitz	Staatl Museum Min. Geol.
Ullmania selaginoides	Brongniart	Staatl Museum Min. Geol.
Ullmania sp.		Naturhistorisches Museum Schloss Bartholdsburg
Unidentified Otovice	Broumova id	Czech Geological Survey
Unidentified Otovice	Broumova id	Czech Geological Survey
Unidentified Otovice	Broumova id	Czech Geological Survey
Unidentified Otovice		Czech Geological Survey
Unidentified Otovice		Czech Geological Survey
Unlabaled		Museum fur Naturkunde
Unlabaled		Museum fur Naturkunde
Voltzia (cf heterophylla?)	Geinitz	Museum der Natur Gotha
Voltzia heterophylla		Museum fur Naturkunde
Voltzia heterophylla		Museum fur Naturkunde
Voltzia liebeana	Geinitz	Staatl Museum Min. Geol.
Voltzia liebeana	Geinitz	Staatl Museum Min. Geol.
Voltzia liebeana	Geinitz	Staatl Museum Min. Geol.
Voltzia liebeana	Geinitz	Staatl Museum Min. Geol.
Voltzia liebeana	Geinitz	Staatl Museum Min. Geol.
Voltzia liebeana	Geinitz	Staatl Museum Min. Geol.
Voltzia liebeana	Geinitz	Staatl Museum Min. Geol.
Voltzia liebeana	Geinitz	Naturhistorisches Museum Schloss Bartholdsburg
Voltzia liebeana ?		Staatl Museum Min. Geol.
Voltzia liebeana ?		Staatl Museum Min. Geol.
Walchia		Naturhistorisches Museum Schloss Bartholdsburg
Walchia		Naturhistorisches Museum Schloss Bartholdsburg
Walchia		Museum der Natur Gotha
Walchia	Sternberg	Naturhistorisches Museum Schloss Bartholdsburg
Walchia (Ernestodendron) arnhadtii	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia (Ernestodendron) arnhadtii	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia (Ernestodendron) arnhadtii	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia (Ernestodendron) arnhadtii	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia (Ernestodendron) arnhadtii	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia ? arnhardtii?		Museum der Natur Gotha
Walchia angustifolia		Czech Geological Survey
Walchia arnhadrtii ?		Museum der Natur Gotha
Walchia arnhadtii	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia arnhadtii	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia arnhadtii	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia arnhadtii	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia arnhadtii ?		Museum der Natur Gotha
Walchia arnhardtii		Museum der Natur Gotha

Walchia arnhardtii		Museum der Natur Gotha
Walchia arnhardtii		Museum der Natur Gotha
Walchia arnhardtii	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia arnhardtii	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia arnhardtii (W. piniformis)		Museum der Natur Gotha
Walchia cf goeppertiana		Czech Geological Survey
Walchia cf laxifolia		Museum der Natur Gotha
Walchia cf piniformis		Staatl Museum Min. Geol.
Walchia cf piniformis		Staatl Museum Min. Geol.
Walchia cf piniformis		Staatl Museum Min. Geol.
Walchia cf piniformis		Staatl Museum Min. Geol.
Walchia cf piniformis		Staatl Museum Min. Geol.
Walchia cf piniformis		Staatl Museum Min. Geol.
Walchia cf piniformis		Staatl Museum Min. Geol.
Walchia cf piniformis		Staatl Museum Min. Geol.
Walchia cf piniformis		Museum fur Naturkunde
Walchia cf piniformis		Museum der Natur Gotha
Walchia cf piniformis		Museum der Natur Gotha
Walchia cf piniformis		Czech Geological Survey
Walchia cf piniformis.		Czech Geological Survey
Walchia filiciformis	Sternberg	Staatl Museum Min. Geol.
Walchia filiciformis	Sternberg	Staatl Museum Min. Geol.
Walchia filiciformis		Museum fur Naturkunde
Walchia filiciformis		Museum fur Naturkunde
Walchia filiciformis	Weissig id	Staatl Museum Min. Geol.
Walchia flaccida o goeppertiana	Florin - Weiss	Narodni Museum
Walchia frondosa		Czech Geological Survey
Walchia frondosa		Czech Geological Survey
Walchia germanica	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia germanica	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia germanica		Naturhistorisches Museum Schloss Bartholdsburg
Walchia germanica		Museum der Natur Gotha
Walchia germanica	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia germanica	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia germanica	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia germanica	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia germanica	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia germanica	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia germanica	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchia germanica or Ernestiodendron		Charles University, Katedra Paleontologie Prirodovedecke Fakalty U K
Walchia goeppertiana	(Florin) Clement-Westerhof	Czech Geological Survey
Walchia goeppertiana	(Florin) Clement-Westerhof	Czech Geological Survey
Walchia goeppertiana	(Florin) Clement-Westerhof	Czech Geological Survey
Walchia goeppertiana		Czech Geological Survey
Walchia goeppertiana		Czech Geological Survey
Walchia goeppertiana		Czech Geological Survey
Walchia goeppertiana		Czech Geological Survey
Walchia goeppertiana		Czech Geological Survey
Walchia goeppertiana		Czech Geological Survey
Walchia hypnoides		Museum fur Naturkunde
Walchia hypnoides		Museum fur Naturkunde
Walchia hypnoides	Feistmantel id	Narodni Museum
Walchia hypnoides	(Brongniart) Broumova	Narodni Museum
Walchia laxifolia		Museum der Natur Gotha
Walchia laxifolia or arnhardtii		Museum der Natur Gotha
Walchia linearifolia	Goeppert	Narodni Museum
Walchia or Ernestiodendron		Charles University, Katedra Paleontologie Prirodovedecke Fakalty U K
Walchia or Ernestiodendron rigidula.		Czech Geological Survey
Walchia parvifolia		Czech Geological Survey
Walchia parvifolia		Czech Geological Survey
Walchia parvifolia		Czech Geological Survey
Walchia parvifolia		Czech Geological Survey
Walchia parvifolia		Czech Geological Survey
Walchia piniformis	(Sternberg) Brogniart	Staatl Museum Min. Geol.
Walchia piniformis		Staatl Museum Min. Geol.
Walchia piniformis	(Schlotheim) Sterberg	Museum fur Naturkunde
Walchia piniformis		Museum fur Naturkunde

Walchia piniformis		Museum fur Naturkunde
Walchia piniformis		Museum fur Naturkunde
Walchia piniformis		Museum fur Naturkunde
Walchia piniformis		Museum fur Naturkunde
Walchia piniformis		Museum fur Naturkunde
Walchia piniformis		Museum fur Naturkunde
Walchia piniformis	(Schlotheim) Sternberg	Museum der Natur Gotha
Walchia piniformis	(Schlotheim) Sternberg	Museum der Natur Gotha
Walchia piniformis		Museum der Natur Gotha
Walchia piniformis		Museum der Natur Gotha
Walchia piniformis		Museum der Natur Gotha
Walchia piniformis		Museum der Natur Gotha
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Walchia piniformis		Museum der Natur Gotha
Walchia piniformis		Museum der Natur Gotha
Walchia piniformis		Museum der Natur Gotha
Walchia piniformis		Czech Geological Survey
Walchia piniformis		Czech Geological Survey
Walchia piniformis		Czech Geological Survey
Walchia piniformis		Museum fur Naturkunde
Walchia piniformis		Czech Geological Survey
Walchia piniformis		Czech Geological Survey
Walchia piniformis	Broumova id	Narodni Museum
Walchia piniformis		Narodni Museum
Walchia piniformis		Czech Geological Survey
Walchia piniformis		Czech Geological Survey
Walchia piniformis		Czech Geological Survey
Walchia piniformis	Sternberg	Charles University, Katedra Paleontologie Prirodovedecke Fakalty U K
Walchia piniformis		Charles University, Katedra Paleontologie Prirodovedecke Fakalty U K
Walchia piniformis		Naturhistorisches Museum Schloss Bartholdsburg
Walchia piniformis also W hypnoides		Museum fur Naturkunde
Walchia piniformis also W hypnoides		Museum fur Naturkunde
Walchia piniformis var linearifolia	Sternberg	Naturhistorisches Museum Schloss Bartholdsburg
Walchia sp or Ernestiodendron filiciforme		Czech Geological Survey
Walchia sp.		Staatl Museum Min. Geol.
Walchia sp.		Naturhistorisches Museum Schloss Bartholdsburg
Walchia sp.		Naturhistorisches Museum Schloss Bartholdsburg
Walchia sp.		Naturhistorisches Museum Schloss Bartholdsburg
Walchia sp.		Czech Geological Survey
Walchia sp.		Czech Geological Survey
Walchia sp.		Czech Geological Survey
Walchia sp.		Czech Geological Survey
Walchia sp.		Czech Geological Survey
Walchia sp.		Czech Geological Survey
Walchia sp.		Czech Geological Survey
Walchia sp.		Naturhistorisches Museum Schloss Bartholdsburg
Walchia sp. 6		Czech Geological Survey
Walchia sp. A		Czech Geological Survey
Walchia sp., Walchia cf arnhadtii		Naturhistorisches Museum Schloss Bartholdsburg
Walchia speciosa		Charles University, Katedra Paleontologie Prirodovedecke Fakalty U K
Walchian conifer		Museum fur Naturkunde
Walchian conifer		Museum fur Naturkunde
Walchianthus sp.		Naturhistorisches Museum Schloss Bartholdsburg
Walchianthus sp.		Naturhistorisches Museum Schloss Bartholdsburg
Walchianthus sp.		Naturhistorisches Museum Schloss Bartholdsburg
Walchianthus sp.	Florin	Naturhistorisches Museum Schloss Bartholdsburg
Walchiostrobus elongatus		Czech Geological Survey
Walchiostrobus sp.		Czech Geological Survey

Species authority indicated only when previous researchers have identified individual specimens. Specimens with more than one species name have no authority name. All specimens have been digitized and most specimens have at least two digital pictures showing a general view of the specimen and a close up. Close ups include areas such as: 1) leaves on penultimate and ultimate shoots; 2) pollen cone bases and microsporophylls; 3) ovulate cone bases and axillary dwarf shoots; and 4) seeds.

Appendix 3. Condensed measurements of five lateral branches from a single node of a juvenile tree of *Araucaria heterophylla* (Salisb.) Franco.

	BR1U1	**BR1U2**	**BR1U3**	**BR1U4**	**BR1U5**	**BR2U1**	**BR2U2**	**BR2U3**	**BR2U4**	**BR2U5**	**BR3U1**	**BR3U2**
DUBx	2.000					2.408					1.887	
DUBs	0.746					0.664					0.178	
DUAx	1.200					1.020					1.217	
DUAs	0.436					0.091					0.233	
LBUx	6.115	8.499	7.724	9.499	6.164	4.047	5.883	6.166	10.174	7.022	7.976	7.131
LBUs	0.547	0.594	0.929	1.246	0.538	0.588	1.028	0.685	2.441	0.575	1.097	0.018
TBUx	1.414	1.488	1.281	1.720	1.442	0.894	1.265	1.281	1.133	1.378	1.414	1.281
TBUs	0.149	0.135	0.244	0.313	0.161	0.100	0.306	0.108	0.158	0.051	0.071	0.000
A1Bx	61.609	67.543	66.954	52.595	44.429	64.006	59.252	79.413	58.838	65.537	65.327	70.143
A1Bs	11.191	7.649	1.968	11.028	2.603	5.610	9.385	1.575	4.721	10.525	4.095	6.244
A2Bx	56.712	63.604	67.543	59.894	48.470	59.094	63.435	80.910	62.852	62.606	65.722	72.510
A2Bs	11.152	6.948	3.115	10.692	3.025	4.276	6.402	7.771	6.281	11.544	3.190	3.107
LAUx	6.128	5.639	6.658	5.969	7.850	7.414	6.090	5.836	5.992	9.072		5.246
LAUs	0.554	0.926	0.840	0.012	1.843	0.793	1.533	1.086	0.752	0.505		0.044
TBUx	1.000	0.861	1.039	1.273	1.342	1.217	0.957	1.265	1.077	1.209		1.166
TBUs	0.066	0.261	0.192	0.011	0.177	0.328	0.089	0.236	0.163	0.187		0.183
A1Ax	55.643	52.563	50.078	61.831	60.255	58.225	71.351	48.504	55.559	47.304		62.603
A1As	4.576	6.431	6.572	3.690	6.096	6.659	14.933	7.796	6.978	15.071		6.926
A2Ax	53.015	54.199	54.405	63.711	60.714	57.851	72.724	46.736	57.095	53.077		58.029
A2As	4.253	6.105	6.237	2.509	18.008	4.448	8.993	4.334	8.391	4.219		4.598

	BR3U3	**BR3U4**	**BR3U5**	**BR4U1**	**BR4U2**	**BR4U3**	**BR4U4**	**BR4U5**	**BR5U1**	**BR5U2**	**BR5U3**	**BR5U4**
DUBx				2.668					2.973			
DUBs				0.314					0.664			
DUAx				1.281					1.281			
DUAs				0.191					0.276			
LBUx	6.240	6.278	4.424	9.032	8.916	9.552	13.308	8.179	11.019	8.476	9.000	11.244
LBUs	0.320	0.862	0.428	0.744	2.495	1.507	2.470	0.908	2.646	2.238	1.610	2.088
TBUx	1.077	1.039	1.139	1.361	1.943	1.483	2.000	1.933	1.577	1.361	1.523	1.720
TBUs	0.000	0.115	0.200	0.207	0.272	0.272	0.306	0.066	0.231	0.114	0.189	0.189
A1Bx	85.513	74.927	60.717	64.523	69.062	74.282	65.695	64.355	64.618	68.240	68.664	57.483
A1Bs	16.423	10.945	4.529	8.436	6.327	7.559	3.144	9.653	6.172	2.513	8.712	6.013
A2Bx	79.047	70.723	62.511	68.928	65.343	72.343	73.262	62.294	66.919	66.795	68.898	67.337
A2Bs	13.886	11.504	8.738	5.550	4.903	4.924	8.001	11.315	3.096	2.594	6.460	9.892
LAUx	5.832	5.445	6.643	8.826	6.719	6.301	7.752	10.172	6.446	7.662	8.639	7.040
LAUs	0.475	0.537	0.784	1.578	0.763	0.507	2.939	1.776	0.798	0.670	0.751	1.063
TBUx	1.191	0.883	1.000	1.311	1.442	1.622	1.550	1.217	1.077	1.789	1.217	1.281
TBUs	0.036	0.400	0.158	0.288	0.209	0.235	0.588	0.184	0.219	0.393	0.111	0.057
A1Ax	50.397	49.246	58.854	49.965	58.423	50.655	53.864	50.711	57.103	70.824	75.964	50.680
A1As	7.632	5.004	15.685	6.566	7.717	7.997	13.221	4.753	9.242	7.251	7.391	9.744
A2Ax	50.420	48.748	60.325	52.808	53.006	49.222	51.964	52.726	57.738	67.963	69.883	50.862
A2As	0.048	8.458	9.265	5.263	6.010	2.942	3.700	5.175	3.848	4.793	3.061	5.909

Totals

	V5Br1	V5Br2	V5Br3	V5Br4	V5Br5
DPBx	5.800	5.800	5.800	5.800	5.800
DPBs	4.804	4.804	4.804	4.804	4.804
DPAx	1.456	1.456	1.456	1.456	1.456
DPAs	0.763	0.763	0.763	0.763	0.763
LPSx	325.707	325.707	325.707	325.707	325.707
LPSs	83.241	83.241	83.241	83.241	83.241
DUBx	2.000	2.408	1.887	2.668	2.973
DUBs	0.746	0.664	0.178	0.314	0.664
DUAx	1.200	1.020	1.217	1.281	1.281
DUAs	0.436	0.091	0.233	0.191	0.276
LBUx	7.600	6.658	6.410	9.797	9.657
LBUs	0.771	1.063	0.545	1.625	2.061
TBUx	1.469	1.190	1.190	1.744	1.618
TBUs	0.200	0.145	0.077	0.225	0.162
A1Bx	58.626	65.409	71.325	67.583	63.708
A1Bs	6.888	6.363	8.447	7.024	5.228
A2Bx	59.245	65.779	70.102	68.434	66.428
A2Bs	6.986	7.255	8.085	6.939	6.356
LAUx	6.449	6.881	5.792	7.954	7.634
LAUs	0.835	0.934	0.460	1.513	0.766
TBUx	1.103	1.145	1.060	1.429	1.366
TBUs	0.141	0.200	0.194	0.301	0.232
A1Ax	56.074	56.189	55.275	52.723	62.782
A1As	5.473	10.287	8.812	8.051	8.803
A2Ax	57.209	57.497	54.380	51.945	61.046
A2As	7.422	6.077	5.592	4.618	4.609

Measurements correspond to the fifth node from the apex to the base of the tree. Each lateral branch (Br1-Br5) and corresponding ultimate shoot (U1-U5) values represent the average (x) and standard deviation (s). All values are in millimeters. Total values are divided in five columns (V1-V5) each showing average values per lateral branch (Br1-Br4). Character abbreviations (DPA, DPB, etc.) as outlined in chapter 2.1.

Appendix 4. All measurements from lateral branches of a juvenile tree of *Araucaria heterophylla* (Salisb.) Franco using the arithmetic mean for each character.

	V1Br1	V1Br2	V1Br3	V1Br4	V1Br5	V2Br1	V2Br2	V2Br3	V2Br4	V2Br5	V3Br1	V3Br2
DPBx	5.667	5.667	5.667	5.667	5.667	6.500	6.500	6.500	6.500	6.500	6.333	6.333
DPBs	0.210	0.210	0.210	0.210	0.210	0.544	0.544	0.544	0.544	0.544	0.461	0.461
DPAx	3.171	3.171	3.171	3.171	3.171	2.138	2.138	2.138	2.138	2.138	1.863	1.863
DPAs	0.170	0.170	0.170	0.170	0.170	0.274	0.274	0.274	0.274	0.274	0.242	0.242
LPSx	132.015	132.015	132.015	132.015	132.015	195.202	195.202	195.202	195.202	195.202	206.432	206.432
LPSs	11.303	11.303	11.303	11.303	11.303	16.764	16.764	16.764	16.764	16.764	17.514	17.514
DUBx	2.744	3.226	2.043	2.165	2.996	2.013	2.404	2.193	1.772	2.571	3.590	3.060
DUBs	0.674	1.928	0.145	0.528	0.077	0.395	0.618	0.564	0.707	0.551	0.705	0.362
DUAx	2.744	1.775	1.213	1.531	1.546	1.414	1.345	1.217	1.281	1.221	1.642	1.572
DUAs	0.674	0.175	0.076	0.274	0.003	0.429	0.195	0.370	0.132	0.227	0.296	0.359
LBUx	11.111	9.722	9.641	10.028	10.654	7.422	7.005	7.615	6.817	7.486	8.113	7.078
LBUs	1.384	1.612	1.628	0.970	0.970	1.132	1.294	0.854	1.164	0.940	0.975	1.133
TBUx	1.679	1.549	1.503	1.506	1.375	1.378	1.376	1.361	1.146	1.266	1.472	1.379
TBUs	0.327	0.120	0.155	0.183	0.172	0.274	0.165	0.301	0.150	0.155	0.269	0.260
A1Bx	49.427	51.859	53.749	63.587	58.232	61.352	68.149	66.517	62.730	63.642	59.807	68.272
A1Bs	9.878	8.830	5.565	5.053	7.453	10.050	8.843	6.508	5.724	6.822	7.183	7.656
A2Bx	51.920	56.093	52.741	64.207	59.475	59.464	62.540	61.724	63.914	63.413	62.209	63.640
A2Bs	7.286	7.740	2.416	4.338	4.874	8.320	7.855	5.002	4.235	6.197	6.583	6.935
LAUx	10.253	11.243	11.650	11.427	12.589	9.041	8.648	8.253	9.056	9.496	9.696	8.448
LAUs	0.728	1.021	1.057	1.350	1.220	1.245	0.728	0.910	1.326	1.604	0.923	0.851
TBUx	0.949	1.813	1.381	1.656	1.573	1.244	1.107	1.108	1.147	1.107	1.324	1.221
TBUs	0.639	0.296	0.225	0.249	0.302	0.226	0.140	0.112	0.180	0.334	0.163	0.193
A1Ax	15.478	47.496	46.658	53.708	51.686	53.531	57.642	58.111	55.503	55.535	55.383	60.676
A1As	8.927	7.923	5.733	5.689	6.578	8.457	10.096	7.693	10.132	7.619	6.830	7.231
A2Ax	28.330	45.895	45.896	52.377	53.596	53.244	58.090	54.438	55.212	58.756	59.280	58.609
A2As	3.496	8.475	9.624	5.041	7.054	6.613	7.986	7.459	7.430	5.261	8.953	5.951

	V3Br3	V3Br4	V3Br5	V4Br1	V4Br2	V4Br3	V4Br4	V4Br5	V5Br1	V5Br2	V5Br3	V5Br4
DPBx	6.333	6.333	6.333	9.690	9.690	9.690	9.690	9.690	5.800	5.800	5.800	5.800
DPBs	0.461	0.461	0.461	1.086	1.086	1.086	1.086	1.086	4.804	4.804	4.804	4.804
DPAx	1.863	1.863	1.863	2.386	2.386	2.386	2.386	2.386	1.456	1.456	1.456	1.456
DPAs	0.242	0.242	0.242	0.266	0.266	0.266	0.266	0.266	0.763	0.763	0.763	0.763
LPSx	206.432	206.432	206.432	312.798	312.798	312.798	312.798	312.798	325.707	325.707	325.707	325.707
LPSs	17.514	17.514	17.514	14.671	14.671	14.671	14.671	14.671	83.241	83.241	83.241	83.241
DUBx	2.357	2.635	2.916	2.953	2.478	2.478	2.667	2.916	2.000	2.408	1.887	2.668
DUBs	0.653	0.606	0.650	0.340	1.066	0.398	0.379	0.802	0.746	0.664	0.178	0.314
DUAx	1.424	1.572	1.414	1.509	1.179	1.269	1.344	1.500	1.200	1.020	1.217	1.281
DUAs	0.250	0.162	0.176	0.158	0.120	0.108	0.718	0.166	0.436	0.091	0.233	0.191
LBUx	6.595	7.548	7.699	8.873	8.097	6.762	7.999	8.352	7.600	6.658	6.410	9.797
LBUs	0.624	1.246	1.015	1.174	1.272	1.306	1.094	0.839	0.771	1.063	0.545	1.625
TBUx	1.289	1.327	1.410	1.608	1.599	1.428	1.679	1.583	1.469	1.190	1.190	1.744
TBUs	0.143	0.225	0.218	0.281	0.318	0.106	0.208	0.229	0.200	0.145	0.077	0.225
A1Bx	63.154	64.174	60.183	68.466	69.956	74.458	64.886	66.490	58.626	65.409	71.325	67.583
A1Bs	6.930	5.807	4.618	9.665	3.845	8.565	9.541	4.857	6.888	6.363	8.447	7.024
A2Bx	60.975	64.986	59.572	66.306	67.511	71.283	64.202	65.044	59.245	65.779	70.102	68.434
A2Bs	4.976	8.079	5.413	7.001	6.299	10.091	7.370	6.343	6.986	7.255	8.085	6.939
LAUx	8.613	8.008	9.553	7.610	6.388	6.319	7.901	7.724	6.449	6.881	5.792	7.954
LAUs	1.181	0.842	1.057	1.253	0.746	0.910	0.894	1.334	0.835	0.934	0.460	1.513
TBUx	1.132	1.189	1.214	1.320	1.329	1.274	1.559	1.354	1.103	1.145	1.060	1.429
TBUs	0.169	0.158	0.191	0.309	0.233	0.264	0.263	0.278	0.141	0.200	0.194	0.301

A1Ax	59.126	64.038	56.248	60.709	51.813	61.086	56.496	58.794	56.074	56.189	55.275	52.723
A1As	5.650	5.299	5.495	5.222	8.379	5.424	8.043	7.747	5.473	10.287	8.812	8.051
A2Ax	58.383	65.988	58.801	56.878	52.608	60.128	56.533	56.796	57.209	57.497	54.380	51.945
A2As	4.629	5.950	5.171	4.585	6.740	3.014	8.714	7.301	7.422	6.077	5.592	4.618

	V5Br5	V6Br1	V6Br2	V6Br3	V6Br4	V6Br5	V6Br6	V6Br7	V7Br1	V7Br2	V7Br3	V7Br4
DPBx	5.800	6.143	6.143	6.143	6.143	6.143	6.143	6.143	4.467	4.467	4.467	4.467
DPBs	4.804	2.228	2.228	2.228	2.228	2.228	2.228	2.228	1.060	1.060	1.060	1.060
DPAx	1.456	1.629	1.629	1.629	1.629	1.629	1.629	1.629	0.904	0.904	0.904	0.904
DPAs	0.763	0.472	0.472	0.472	0.472	0.472	0.472	0.472	0.250	0.250	0.250	0.250
LPSx	325.707	257.114	257.114	257.114	257.114	257.114	257.114	257.114	227.572	227.572	227.572	227.572
LPSs	83.241	45.270	45.270	45.270	45.270	45.270	45.270	45.270	12.454	12.454	12.454	12.454
DUBx	2.973	2.942	2.729	2.657	2.236	1.317	1.491	1.471	1.917	1.857	1.629	1.539
DUBs	0.664	0.520	0.550	0.593	0.958	0.417	0.733	0.471	0.334	0.304	0.222	0.356
DUAx	1.281	1.457	1.355	1.229	1.040	0.606	0.714	1.000	1.152	1.286	1.116	0.915
DUAs	0.276	0.426	0.310	0.103	0.391	0.141	0.265	0.271	0.277	0.221	0.302	0.211
LBUx	9.657	8.560	9.239	8.336	5.843	5.431	6.461	6.286	6.950	7.058	6.917	6.920
LBUs	2.061	1.248	0.742	1.320	0.943	0.515	1.064	0.845	1.155	0.900	1.206	0.815
TBUx	1.618	1.519	1.531	1.496	1.070	0.872	1.063	1.035	1.199	1.038	1.085	1.082
TBUs	0.162	0.451	0.125	0.201	0.084	0.090	0.128	0.201	0.113	0.134	0.163	0.101
A1Bx	63.708	61.184	63.752	56.222	63.966	61.930	65.102	66.498	65.030	66.206	62.099	50.019
A1Bs	5.228	8.431	7.966	6.714	7.290	6.017	7.779	8.538	6.720	9.191	5.566	11.661
A2Bx	66.428	62.140	62.576	59.990	67.003	61.195	65.793	65.575	63.399	65.986	62.409	54.246
A2Bs	6.356	6.647	5.110	6.437	2.008	3.476	6.002	8.877	5.733	9.341	5.358	8.433
LAUx	7.634	7.152	6.345	6.266	4.587	5.220	5.725	5.694	6.214	5.855	5.551	5.774
LAUs	0.766	0.998	0.653	1.026	1.009	0.719	0.812	0.676	0.785	0.689	0.773	0.375
TBUx	1.366	1.357	1.155	1.304	1.077	0.906	0.928	0.870	1.217	1.129	1.030	1.042
TBUs	0.232	0.135	0.182	0.226	0.161	0.138	0.187	0.077	0.133	0.154	0.153	0.136
A1Ax	62.782	55.487	57.660	52.030	51.477	57.723	55.595	59.786	52.091	58.756	57.279	47.792
A1As	8.803	9.940	7.958	11.683	6.931	6.641	10.532	8.992	10.573	7.532	11.949	9.978
A2Ax	61.046	57.950	57.361	51.796	51.438	55.958	57.498	65.847	52.148	56.523	55.432	49.601
A2As	4.609	7.301	5.620	8.237	6.007	6.942	4.844	7.742	7.604	3.997	5.235	7.955

	V8Br1	V8Br2	V8Br3
DPBx	1.644	1.644	1.644
DPBs	1.165	1.165	1.165
DPAx	1.305	1.305	1.305
DPAs	0.075	0.075	0.075
LPSx	168.811	168.811	168.811
LPSs	30.053	30.053	30.053
DUBx	2.226	2.114	1.502
DUBs	0.525	0.740	0.697
DUAx	1.414	1.770	0.875
DUAs	0.202	0.125	0.234
LBUx	8.586	10.304	8.669
LBUs	1.211	2.667	1.374
TBUx	1.346	1.376	1.410
TBUs	0.151	0.176	0.257
A1Bx	74.195	73.417	74.335
A1Bs	8.665	6.441	7.330
A2Bx	73.456	69.670	70.809
A2Bs	7.575	5.353	7.758
LAUx	6.728	6.607	7.231
LAUs	0.575	1.265	0.786

TBUx	1.236	1.232	1.269
TBUs	0.166	0.186	0.173
A1Ax	53.358	47.541	54.156
A1As	4.919	10.203	7.902
A2Ax	51.638	50.520	54.402
A2As	6.329	7.403	6.367

Measurements correspond to the all nodes on the tree (V1-V8), from the apex to the base of the tree. Lateral branch (Br1-Br5) values correspond to the average (x) and standard deviation (s). All values are in millimeters. Character abbreviations (DPA, DPB, etc.) as outlined in chapter 2.1.

Appendix 5. Measurements from a single specimen of *Lebachia piniformis* (Schloth.) Florin used for multivariate analyses.

Specimen	(DUB)	(DUA)	Leaves	(LBU)	(TBU)	(A1B)	(A2B)	(LAU)	(TBU)	(A1A)	(A2A)
	0.176	0.115	Izq. 1	0.378	0.057	40.786	51.806	0.533	0.036	52.651	45
			Izq. 2	0.474	0.051	52.125	67.38	0.283	0.04	50.44	72.15
Taf 3-4_1			Izq. 3	0.454	0.057	41.634	55.934	0.594	0.065	58.912	62.22
Der. R1.			Izq. 4	0.356	0.065	36.545	24.394	0.412	0.054	40.786	46.444
(DPB) 0.613			Izq. 5					0.489	0.04	28.902	49.95
(DPA) 0.487			Der. 1	0.533	0.074	36.614	45.712	0.44	0.09	69.944	74.055
(LPS) 15.822			Der. 2	0.433	0.054	41.84	54.067	0.628	0.054	38.66	39.806
			Der. 3	0.665	0.074	36.114	43.161	0.563	0.04	42.138	38.418
			Der. 4	0.621	0.054	23.769	32.757	0.528	0.051	38.66	40.601
			Der. 5					0.62	0.057	34.019	36.119
	(DUB)	(DUA)	Leaves	(LBU)	(TBU)	(A1B)	(A2B)	(LAU)	(TBU)	(A1A)	(A2A)
Der.R2	0.162	0.127	Izq. 1	0.362	0.074	55.008	72.897				
			Izq. 2	0.408	0.092	52.125	40.135				
			Izq. 3	0.363	0.065	45	42.735				
			Izq. 4	0.363	0.057	40.236	50.315				
			Izq. 5								
			Der. 1	0.438	0.072	36.703	33.453				
			Der. 2	0.51	0.04	42.797	40.752				
			Der. 3	0.595	0.074	40.561	39.566				
			Der. 4								
			Der. 5								
	DUB	(DUA)	Leaves	(LBU)	(TBU)	(A1B)	(A2B)	(LAU)	(TBU)	(A1A)	(A2A)
Der.R3	0.198	0.127	Izq. 1	0.452	0.051	44.465	55.008	0.736	0.072	54.728	60.709
			Izq. 2	0.57	0.057	28.393	32.421	0.529	0.065	63.435	59.47
			Izq. 3	0.403	0.09	51.911	56.634	0.681	0.065	60.725	52.452
			Izq. 4								
			Izq. 5								
			Der. 1					0.551	0.074	37.235	38.509
			Der. 2					0.53	0.057	47.793	51.546
			Der. 3					0.397	0.057	38.904	38.517
			Der. 4					0.587	0.081	36.87	31.629
			Der. 5					0.708	0.04	25.723	36.547
	DUB	(DUA)	Leaves	(LBU)	(TBU)	(A1B)	(A2B)	(LAU)	(TBU)	(A1A)	(A2A)
Der.R4	0.198	0.153	Izq. 1	0.402	0.054	43.995	61.164	0.496	0.09	49.879	54.765
			Izq. 2	0.583	0.072	39.579	40.972	0.422	0.074	47.663	39.588
			Izq. 3	0.615	0.04	37.185	41.055	0.748	0.054	32.642	38.66
			Izq. 4					0.702	0.057	36.027	35.362
			Izq. 5					0.531	0.081	32.005	31.977
			Der. 1	0.519	0.051	57.529	48.93	0.94	0.057	36.87	37.441
			Der. 2	0.997	0.054	35.538	33.736	0.519	0.074	45	39.094
			Der. 3	0.76	0.092	43.464	56.31	0.623	0.074	34.183	41.216
			Der. 4					0.493	0.051	43.493	50.906
			Der. 5					0.697	0.081	38.169	41.912
	DUB	(DUA)	Leaves	(LBU)	(TBU)	(A1B)	(A2B)	(LAU)	(TBU)	(A1A)	(A2A)
Der.R5	0.178	0.115	Izq.1	0.441	0.072	34.909	39.699	0.398	0.054	71.565	59.036
			Izq. 2	0.358	0.054	36.327	35.407	0.57	0.092	35.538	48.366
			Izq. 3	0.516	0.057	45	24.775	0.312	0.072	37.185	36.626
			Izq. 4					0.329	0.057	40.815	40.236
			Izq. 5								
			Der. 1	0.542	0.057	33.69	43.854	0.618	0.074	33.977	46.79
			Der. 2	0.68	0.065	34.234	43.807	0.461	0.065	50.389	42.13
			Der. 3	0.686	0.057	35.599	46.012	0.555	0.036	42.58	50.194
			Der. 4					0.592	0.054	33.147	50.356
NUS16			Der. 5					0.594	0.057	51.34	38.454
	DUB	(DUA)	Leaves	(LBU)	(TBU)	(A1B)	(A2B)	(LAU)	(TBU)	(A1A)	(A2A)
Izq.R1	0.163	0.102	Izq. 1	0.393	0.061	38.66	59.931	0.437	0.057	48.668	41.702
			Izq. 2	0.446	0.091	54.52	48.434	0.434	0.073	48.965	54.462
			Izq. 3	0.557	0.061	53.344	46.685	0.487	0.118	49.268	42.064
			Izq. 4	0.554	0.086	44.236	43.675	0.393	0.064	36.87	41.444
			Izq. 5					0.689	0.045	36.87	38.917
			Der. 1	0.453	0.061	44.293	28.25	0.596	0.061	41.371	33.69
			Der. 2	0.634	0.081	34.032	33.538	0.585	0.061	46.397	39.936
			Der. 3	0.463	0.061	40.815	51.546	0.555	0.064	56.31	34.496
			Der. 4					0.714	0.061	37.057	42.429
			Der. 5								
	DUB	(DUA)	Leaves	(LBU)	(TBU)	(A1B)	(A2B)	(LAU)	(TBU)	(A1A)	(A2A)
Izq.R2	0.124	0.102	Izq. 1	0.649	0.084	25.994	35.746	0.879	0.061	17.364	47.121
			Izq. 2	0.495	0.084	45	35.245	0.829	0.045	30.256	36.433
			Izq. 3	0.521	0.102	44.215	37.765	0.631	0.064	34.306	39.094
			Izq. 4					0.619	0.061	42.709	45.448

			Izq. 5								
			Der. 1	0.529	0.064	35.362	27.144	0.639	0.045	32.699	40.641
			Der. 2	0.663	0.045	33.83	53.13	0.555	0.061	29.871	32.905
			Der. 3	0.605	0.061	71.211	43.854	0.795	0.064	32.471	24.848
NUS	**20**	**ramas**	**Der. 4**	0.611	0.041	38.9	36.741	0.56	0.061	36.87	37.648

Totals	FLP2
DPB	0.613
DPA	0.487
LPS	15.822
DUB	0.171
DUA	0.120
NUS	36.000
LBU	0.524
LAU	0.570
TBU	0.065
TAU	0.062
A1B	41.547
A1A	42.061
A2B	44.012
A2A	43.899

Character abbreviations (DPA, DPB, etc.) as outlined in chapter 2.1. Der.R = ultimate shoot found on the right side of the specimen. Izq.R = ultimate shoot found on the left of the specimen. Der.1-5.= leaves on the right side of the ultimate shoot. Izq.1-5 = leaves on the left side of the ultimate shoot. Total values for the specimen indicated as "Totals". FLP2 = abbreviation for the specimen.

Appendix 6. Measurements from a single specimen of *Ernestiodendron filiciforme* Florin used for multivariate analyses.

Specimen	DUB	(DUA)	Leaves	(LBU)	(TBU)	(A1B)	(A2B)	(LAU)	(TBU)	(A1A)	(A2A)
	0.198	0.131	Izq. 1	0.329	0.04	132.709	121.139	0.497	0.04	84.644	111.371
			Izq. 2	0.405	0.046	114.228	149.859	0.426	0.04	64.29	92.203
Gr3Ber06			Izq. 3	0.254	0.052	120.964	135	0.461	0.025	65.095	72.897
Der.R1			Izq. 4					0.47	0.025	72.867	92.121
			Izq. 5								
(DPB) 0.636			Der. 1	0.404	0.051	98.509	107.526	0.35	0.028	100.125	104.036
(DPA) 0.70			Der. 2	0.547	0.038	97.997	112.011	0.653	0.025	79.695	79.216
(LPS) 7.039			Der. 3	0.288	0.025	76.504	93.013	0.69	0.046	81.324	92.705
			Der. 4	0.507	0.04	94.764	95.599	0.358	0.038	98.13	83.83
			Der. 5	0.256	0.051	116.565	90	0.546	0.025	86.82	111.943
	DUB	(DUA)	Leaves	(LBU)	(TBU)	(A1B)	(A2B)	(LAU)	(TBU)	(A1A)	(A2A)
Der. R2	0.17	0.131	Izq. 1	0.403	0.064	95.497	100.305	0.595	0.04	77.361	78.179
			Izq. 2	0.61	0.025	79.205	92.153	0.566	0.028	95.08	83.199
			Izq. 3	0.571	0.038	84.623	101.634	0.552	0.04	84.806	92.877
			Izq. 4	0.438	0.025	85.03	80.665	0.467	0.04	86.077	94.635
			Izq. 5								
			Der. 1	0.655	0.052	102.791	115.346	0.643	0.04	77.005	81.534
			Der. 2	0.622	0.052	93.945	131.634	0.599	0.038	87.274	72.408
			Der. 3	0.361	0.051	98.881	118.836	0.554	0.051	71.704	87.839
			Der. 4	0.796	0.04	74.476	98.13	0.527	0.04	61.113	77.687
			Der. 5	0.477	0.051	108.435	88.433	0.562	0.04	90.483	83.639
	DUB	(DUA)	Leaves	(LBU)	(TBU)	(A1B)	(A2B)	(LAU)	(TBU)	(A1A)	(A2A)
Der. R3	0,14	0.109	Izq. 1	0.573	0.036	95.194	103.314				
			Izq. 2	0.422	0.028	90.69	74.539				
			Izq. 3	0.455	0.038	92.386	115.292				
			Izq. 4	0.28	0.036	133.025	96.116				
			Izq. 5	0.362	0.036	76.759	74.055				
			Der. 1	0.601	0.036	88.295	101.441				
			Der. 2	0.509	0.04	97.125	88.172				
			Der. 3	0.497	0.036	91.287	90				
			Der. 4								
			Der. 5								
	DUB	(DUA)	Leaves	(LBU)	(TBU)	(A1B)	(A2B)	(LAU)	(TBU)	(A1A)	(A2A)
Der. R4	0.188		Izq. 1	0.421	0.038	75.53	93.621				
			Izq. 2	0.52	0.038	99.162	79.019				
			Izq. 3	0.333	0.028	102.579	91.705				
			Izq. 4	0.479	0.057	88.335	85.601				
			Izq. 5	0.536	0.046	91.005	106.25				
			Der. 1	0.421	0.028	92.816	83.454				
			Der. 2	0.561	0.038	75.76	95.297				
			Der. 3	0.418	0.04	98.13	82.196				
NUS 5			Der. 4	0.613	0.038	91.245	93.832				

Totals	[illegible]
DPB	0.636
DPA	0.7
LPS	7.039
DUB	0.173
DUA	0.124
NUS	5.000
LBU	0.468
LAU	0.529
TBU	0.041
TAU	0.036
A1B	95.719
A1A	81.327
A2B	99.564
A2A	88.462

Character abbreviations (DPA, DPB, etc.) as outlined in chapter 2.1. Der.R = ultimate shoot found on the right side of the specimen. Izq.R = ultimate shoot found on the left of the specimen. Der.1-5.= leaves on the right side of the ultimate shoot. Izq.1-5 = leaves on the left side of the ultimate shoot. Total values for the specimen indicated as "Totals". FLP2 = abbreviation for the specimen.

Appendix 7. Data matrix used for principal component analyses. Portions of this matrix were used to analyzed individual data sets (*T. mahoningensis*, specimens from Europe, and *A. heterophylla*). All measurements in millimeters.

75 Taxa

14.00 Chars.

Taxa	Q DPBx	Q DPAx	Q LPSx	Q DUBx	Q DUAx	Q LBUx	Q TBUx	Q A1Bx	Q A2Bx	Q LAUx	Q TBUx	Q A1Ax	Q A2Ax	Q MUS
V1Br1	5.67	3.17	132.01	2.74	2.74	11.11	1.68	49.43	51.92	10.25	0.95	15.48	28.33	6
V1Br2	5.67	3.17	132.01	3.23	1.77	9.72	1.55	51.86	56.09	11.24	1.81	47.50	45.90	4
V1Br3	5.67	3.17	132.01	2.04	1.21	9.64	1.50	53.75	52.74	11.65	1.38	46.66	45.90	6.00
V1Br4	5.67	3.17	132.01	2.16	1.53	10.03	1.51	63.59	64.21	11.43	1.66	53.71	52.38	7.00
V1Br5	5.67	3.17	132.01	3.00	1.55	10.65	1.38	58.23	59.47	12.59	1.57	51.69	53.60	8.00
V2Br1	6.50	2.14	195.20	2.01	1.41	7.42	1.38	61.35	59.46	9.04	1.24	53.53	53.24	15.00
V2Br2	6.50	2.14	195.20	2.40	1.35	7.01	1.38	68.15	62.54	8.65	1.11	57.64	58.09	18.00
V2Br3	6.50	2.14	195.20	2.19	1.22	7.61	1.36	66.52	61.72	8.25	1.11	58.11	54.44	19.00
V2Br4	6.50	2.14	195.20	1.77	1.28	6.82	1.15	62.73	63.91	9.06	1.15	55.50	55.21	12.00
V2Br5	6.50	2.14	195.20	2.57	1.22	7.49	1.27	63.64	63.41	9.50	1.11	55.53	58.76	18.00
V3Br1	6.33	1.86	206.43	3.59	1.64	8.11	1.47	59.81	62.21	9.70	1.32	55.38	59.28	15.00
V3Br2	6.33	1.86	206.43	3.06	1.57	7.08	1.38	68.27	63.64	8.45	1.22	60.68	58.61	18.00
V3Br3	6.33	1.86	206.43	2.36	1.42	6.59	1.29	63.15	60.97	8.61	1.13	59.13	58.38	19.00
V3Br4	6.33	1.86	206.43	2.63	1.57	7.55	1.33	64.17	64.99	8.01	1.19	64.04	65.99	12.00
V3Br5	6.33	1.86	206.43	2.92	1.41	7.70	1.41	60.18	59.57	9.55	1.21	56.25	58.80	18.00
V4Br1	9.69	2.39	312.80	2.95	1.51	8.87	1.61	68.47	66.31	7.61	1.32	60.71	56.88	28.00
V4Br2	9.69	2.39	312.80	2.48	1.18	8.10	1.60	69.96	67.51	6.39	1.33	51.81	52.61	27.00
V4Br3	9.69	2.39	312.80	2.48	1.27	6.76	1.43	74.46	71.28	6.32	1.27	61.09	60.13	26.00
V4Br4	9.69	2.39	312.80	2.67	1.34	8.00	1.68	64.89	64.20	7.90	1.56	56.50	56.53	27.00
V4Br5	9.69	2.39	312.80	2.92	1.50	8.35	1.58	66.49	65.04	7.72	1.35	58.79	56.80	28.00
V5Br1	5.80	1.46	325.71	2.00	1.20	7.60	1.47	58.63	59.24	6.45	1.10	56.07	57.21	39.00
V5Br2	5.80	1.46	325.71	2.41	1.02	6.66	1.19	65.41	65.78	6.88	1.14	56.19	57.50	31.00
V5Br3	5.80	1.46	325.71	1.89	1.22	6.41	1.19	71.32	70.10	5.79	1.06	55.28	54.38	35.00
V5Br4	5.80	1.46	325.71	2.67	1.28	9.80	1.74	67.58	68.43	7.95	1.43	52.72	51.94	36.00
V5Br5	5.80	1.46	325.71	2.97	1.28	9.66	1.62	63.71	66.43	7.63	1.37	62.78	61.05	38.00
V6Br1	6.14	1.63	257.11	2.94	1.46	8.56	1.52	61.18	62.14	7.15	1.36	55.49	57.95	23.00
V6Br2	6.14	1.63	257.11	2.73	1.36	9.24	1.53	63.75	62.58	6.34	1.15	57.66	57.36	28.00
V6Br3	6.14	1.63	257.11	2.66	1.23	8.34	1.50	56.22	59.99	6.27	1.30	52.03	51.80	29.00
V6Br4	6.14	1.63	257.11	2.24	1.04	5.84	1.07	63.97	67.00	4.59	1.08	51.48	51.44	21.00
V6Br5	6.14	1.63	257.11	1.32	0.61	5.43	0.87	61.93	61.19	5.22	0.91	57.72	55.96	18.00
V6Br6	6.14	1.63	257.11	1.49	0.71	6.46	1.06	65.10	65.79	5.72	0.93	55.60	57.50	20.00
V6Br7	6.14	1.63	257.11	1.47	1.00	6.29	1.03	66.50	65.57	5.69	0.87	59.79	65.85	21.00
V7Br1	4.47	0.90	227.57	1.92	1.15	6.95	1.20	65.03	63.40	6.21	1.22	52.09	52.15	18.00
V7Br2	4.47	0.90	227.57	1.86	1.29	7.06	1.04	66.21	65.99	5.86	1.13	58.76	56.52	12.00
V7Br3	4.47	0.90	227.57	1.63	1.12	6.92	1.09	62.10	62.41	5.55	1.03	57.28	55.43	13.00
V7Br4	4.47	0.90	227.57	1.54	0.92	6.92	1.08	50.02	54.25	5.77	1.04	47.79	49.60	15.00
V8Br1	1.64	1.30	168.81	2.23	1.41	8.59	1.35	74.19	73.46	6.73	1.24	53.36	51.64	3.00
V8Br2	1.64	1.30	168.81	2.11	1.77	10.30	1.38	73.42	69.67	6.61	1.23	47.54	50.52	2.00
V8Br3	1.64	1.30	168.81	1.50	0.88	8.67	1.41	74.33	70.81	7.23	1.27	54.16	54.40	4.00
ThG1	3.00	2.00	73.00	1.00	0.76	19.00	4.14	4.00	0.45	0.46	40.25	50.00	40.00	48.00
ThG4	4.00	3.00	72.00	1.00	0.76	37.00	4.62	3.90	0.52	0.54	43.12	33.50	30.50	43.70
ThG10	2	3.00	54.00	1.00	0.75	18.00	4.30	3.47	0.51	0.51	34.05	43.20	36.00	46.15
ThG15	5.00	4.00	82.00	1.00	0.74	7.00	4.84	4.44	0.41	0.42	33.95	47.1	27.8	41.68
ThG16	3.00	3.00	62.00	1.08	0.60	7.00	5.45	4.31	0.46	0.45	33.42	48.10	28.6	43.00
ThGm2	6.00	4.00	153.00	1.90	1.10	43.00	4.39	3.91	0.52	0.59	37.08	48.30	31.9	44.18
ThG8	4.00	1.00	93.00	1.00	7.00	62.00	4.66	4.12	0.43	0.41	26.40	38.40	29.06	40.88
ThG48	3.00	3.00	52.00	1.26	0.88	7.00	5.29	4.43	0.57	0.67	29.82	46.59	26.64	41.79
ThG25	1.00	0.50	41.00	1.00	0.85	13.00	3.44	3.57	0.54	0.64	35.40	47.53	35.75	49.50
ThG27	1.00	1.00	18.00	1.00	1.02	6.00	4.00	4.25	0.55	0.56	30.06	44.37	31.2	45.40
ThG205	7	4.00	140.00	1	1.08	36	4.82	4.6	0.52	0.53	33.1	42.25	30.54	42.46
ThG190	2.20	99.00	98	1	1.24	6	4.52	4.72	0.47	0.51	39.14	47.86	35.18	47.23
ThG158	5.00	99.00	51.00	2.00	1.85	5.00	3.58	3.94	0.47	0.49	31.87	43.37	35	45.1
FML3	0.56	0.18	16.35	0.18	0.21	33.00	0.32	0.33	0.06	0.10	67.20	62.91	72.3	67.49
FML2	1.50	0.72	29.83	0.16	0.12	23.00	0.58	0.63	0.09	0.09	68.82	58.86	67.83	65.34
FML1	0.52	0.53	13.30	0.13	0.08	6.00	0.66	0.66	0.06	0.05	58.63	71.68	59.10	69.17

FEFB	0.64	0.70	7.04	0.17	0.12	5.00	0.47	0.53	0.04	0.04	95.72	81.33	99.56	88.46
FEFB1	0.43	0.18	4.68	0.18	0.13	3.23	0.46	0.53	0.41	0.04	92.36	81.23	99.25	23.00
FEFB2	0.43	0.14	17.41	0.11	0.12	4.24	0.46	0.54	0.41	0.04	94.26	81.26	99.25	31.00
FEFB3	0.47	0.11	9.57	0.11	0.08	4.25	0.46	0.54	0.42	0.04	94.26	82.01	99.46	43.00
FEFB4	0.23	0.56	9.40	0.11	0.08	4.21	0.45	0.54	0.42	0.04	93.56	81.89	99.53	44.00
FEFB5	0.77	0.43	20.17	0.19	0.13	4.34	0.61	0.56	0.42	0.04	93.12	81.34	99.56	61.00
FEFB6	0.49	0.30	7.59	0.18	0.13	4.35	0.62	0.57	0.42	0.04	93.26	81.44	99.57	36.00
FML4	0.72	0.36	10.18	0.17	0.11	14.00	0.61	0.63	0.07	0.07	49.13	50.72	51.53	50.81
FLP1	1.23	0.76	7.59	0.17	0.12	7.00	0.48	0.39	0.06	0.06	34.71	40.32	47.61	53.43
FLP2	0.61	0.49	15.82	0.17	0.12	36.00	0.52	0.57	0.07	0.06	41.55	42.06	44.01	43.90
FLP3	0.79	0.51	9.37	0.08	0.05	31.00	0.49	0.34	0.05	0.05	33.75	40.63	38.27	44.38
FLP4	0.50	0.47	10.35	0.11	0.08	25.00	0.51	0.42	0.05	0.05	37.91	44.14	42.45	42.76
FLP5	1.44	0.87	9.06	0.12	0.07	18.00	0.53	0.43	0.06	0.06	34.53	33.65	40.17	39.23
FLP6	0.81	0.43	10.91	0.11	0.05	18.00	0.31	0.31	0.04	0.04	41.88	47.25	45.75	47.41
FLP7	1.05	0.70	6.00	0.08	0.05	17.00	0.53	0.45	0.05	0.06	42.65	42.35	46.42	46.30
FLP8	0.27	0.21	5.30	0.07	0.05	21.00	0.41	0.37	0.05	0.05	37.47	39.67	40.32	39.57
FLP9	0.70	0.65	6.47	0.11	0.07	16.00	0.58	0.55	0.06	0.06	41.55	37.23	48.09	42.37
FLP10	0.21	0.09	7.41	0.10	0.06	20.00	0.55	0.43	0.05	0.06	29.58	35.76	34.23	33.04
FLP11	0.81	0.17	17.92	0.09	0.06	14.00	0.37	0.36	0.05	0.05	35.59	36.35	45.97	44.3
FLP12	0.80	0.50	15.17	0.10	0.06	51.00	0.43	0.35	0.05	0.05	44.24	47.75	47.62	52.13

Abbreviations: V = node and Br= lateral branch on *A. heterophylla* tree. Nodes range from V1 to V8 and lateral branches from Br1 to Br7. ThG = individual specimens of *T. mahoningensis*. FML = specimens from Montpellier, France; FEFB = *E. filiciforme* specimens; FLP = *L. piniformis* specimens. Character abbreviations as outlined in chapter 2.1. All values in millimeters.